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The genus *Plagiochila* (Dumort.) Dumort.  
(Marchantiophyta) in Madagascar

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# The genus *Plagiochila* (Dumort.) Dumort. (Marchantiophyta) in Madagascar

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## ABSTRACT

*Plagiochila* (Dumort.) Dumort. is one of the largest liverwort genera of Madagascar. A study of the rich *Plagiochila* holdings from Madagascar kept in the herbaria of Brussels, Eger and Paris leads to the recognition of 22 species, in six sections. One species, *P. vandenberghenii* Gradst., sp. nov., is new to science and *P. bifaria* (Sw.) Lindenb., *P. macrostachya* Lindenb. (synonym: *P. granditexta* Steph. syn. nov.) and *P. simplex* (Sw.) Lindenb., all three from the Neotropics, are recorded for the first time from Africa. Madagascar harbors about half of the African *Plagiochilas* and three species are endemic, *P. fracta* Pócs, *P. sikorae* Steph. and *P. vandenberghenii* Gradst., sp. nov. The high *Plagiochila* richness of Madagascar is explained by the large tracts on the island of humid tropical montane forest, being the preferred habitat of the genus. East African and Afro-American taxa prevail and four species, *P. bifaria*, *P. macrostachya*, *P. simplex* and *P. stricta* Lindenb., have a peri-Afro-American range being absent on the African mainland. A key to the Madagassan species of *Plagiochila* is provided and each species is described and illustrated, with data on types, synonyms, geographical distribution, habitat and differentiating characters.

**KEY WORDS**  
Plagiochilaceae,  
Madagascar,  
liverworts,  
lectotypification,  
new records,  
new combination,  
new species.

## RÉSUMÉ

*Le genre Plagiochila (Dumort.) Dumort. (Marchantiophyta) à Madagascar.*

Le genre *Plagiochila* (Dumort.) Dumort. est l'un des plus grands genres d'hépatiques à Madagascar. Une étude des riches collections malgaches de *Plagiochila* conservées dans les herbiers de Bruxelles, Eger et Paris conduit à la reconnaissance de 22 espèces, réparties en six sections. *Plagiochila vandenberghenii* Gradst., sp. nov. est nouvelle pour la science, tandis que *P. bifaria* (Sw.) Lindenb., *P. macrostachya* Lindenb. (synonyme : *P. granditexta* Steph. syn. nov.) et *P. simplex* (Sw.) Lindenb., toutes trois de l'Amérique tropicale, sont enregistrées pour la première fois en Afrique. Madagascar possède environ la moitié de toutes les espèces de *Plagiochila* connues de l'Afrique et trois espèces sont endémiques, *P. fracta* Pócs, *P. sikorae* Steph. et *P. vandenberghenii* Gradst., sp. nov. La richesse en *Plagiochila*

**MOTS CLÉS**  
 Plagiochilaceae,  
 Madagascar,  
 hépatoïques,  
 lectotypification,  
 signalements nouveaux,  
 combinaison nouvelle,  
 espèce nouvelle.

de Madagascar s'explique par les grandes étendues de forêt tropicale humide de montagne sur l'île, habitat préféré du genre. Les taxons est-africains et afro-américains prédominent et quatre espèces, *P. bifaria*, *P. macrostachya*, *P. simplex* et *P. stricta* Lindenb., ont une répartition péri-afro-américaine, étant absentes sur le continent africain. Une clé des espèces malgaches de *Plagiochila* est fournie et chaque espèce est décrite et illustrée, avec des données sur les types, les synonymes, la distribution géographique, l'habitat et les caractères distinctifs.

## INTRODUCTION

*Plagiochila* (Dumort.) Dumort. (Plagiochilaceae) is one of the largest genera of liverworts with about 400-450 species worldwide (Heinrichs 2002; Gradstein 2016). The bulk of the species are from America and Asia (Inoue 1989; Crosby & Engel 2006), fewer occur in Africa where 76 species are recorded (Wigginton 2018). The majority of the African *Plagiochilas* remain insufficiently known, and about half of the species have not been treated in recent taxonomic studies (Wigginton 2018). Heinrichs *et al.* (2005a) accepted *c.* 40 species in Africa.

The present paper deals with the species of *Plagiochila* in Madagascar. The first record has been *Plagiochila dichotoma* var. *laxa* Gottsche, Lindenb. & Nees, which was reported from Madagascar by Gottsche *et al.* (1844) in the *Synopsis Hepaticarum*. According to Grolle (1995), the material belongs to *P. integerrima* Steph., a species widespread in tropical Africa but not common in Madagascar. The second record was *P. mascarena* (Gottsche 1857), a rare taxon of Madagascar and the Mascarene Islands, now called *P. punctata* var. *paucidentata* (Mont. & Gottsche) Gradst., comb. nov.

The first major contribution was by Gottsche (1882) who described nine *Plagiochila* species from Madagascar, all of them new to science: *P. borgenii* Gottsche (synonym of *P. terebrans* Lindenb.), *P. kiaeri* Gottsche, *P. laxifolia* Gottsche (synonym of *P. terebrans* ?), *P. madagascariensis* Gottsche (synonym of *P. repanda* [Schwägr.] Lindenb.), *P. nemophila* Gottsche (synonym of *P. incerta* Gottsche), *P. nudiuscula* Gottsche (synonym of *P. repanda*), *P. pallida* Gottsche (synonym of *P. angusta* Lindenb.), *P. rutenbergiana* Gottsche (synonym of *P. repanda*) and *P. sublinearis* Gottsche (synonym of *P. terebrans*). Based on our knowledge they belong to five different species and some of these, including *P. repanda* and *P. terebrans*, were described multiple times. All are common species of Madagascar. Mitten (1886) added two further species, *P. dicrana* Mitt. and *P. crispulocaudata* Mitt., which are now named *P. drepanophylla* Sande Lac. and *P. squamulosa* Mitt., respectively.

The largest number of *Plagiochila* species was reported by Stephani (1890, 1891, 1892a, 1892b, 1893, 1906), who described over twenty species from Madagascar, almost all of them new to science. However, only five species, *P. boryana* Steph., *P. cambouena* Steph., *P. granditexta* Steph., *P. perrotana* Steph. and *P. sikorae* Steph., were genuine new records (the remaining ones had already been reported from Madagascar under other names) and only two of the new species, *P. bory-*

*ana* and *P. sikorae*, are currently accepted, the rest (90%) are synonyms. Dugas (1928) added *P. undulata* Dugas, which was a synonym of the widespread Afro-American *P. corrugata* (Grolle 1995; Heinrichs *et al.* 2005b). In total, 14 currently accepted species of *Plagiochila* had been reported from Madagascar by the early 20<sup>th</sup> century. A further 22 recorded species were ill-founded and are now considered synonyms.

All species hitherto known from Madagascar were described by Jones (1962) in his important revision of African *Plagiochila*. However, very few collections from Madagascar, belonging to four or five species only (*P. barteri*, *P. integerrima*, *P. squamulosa*, *P. terebrans*; possibly *P. heterostipa*), were included in that study. The first major taxonomic treatment based on a large amount of material from Madagascar was published by Vanden Berghen (1981). The paper presented descriptions, illustrations and a key to sixteen species of Madagascar, with notes on type specimens, habitat, distribution, etc. The nomenclature of the species was subsequently updated by Grolle (1995) in the framework of a detailed revision of the types of all liverworts recorded from the East African islands.

The works by Vanden Berghen and Grolle have been the basis for our current knowledge of *Plagiochila* in Madagascar. In this century, two further species have been added to the flora of Madagascar, *P. fracta* Pócs (Pócs & Geissler 2002; Pócs 2015) and *P. stricta* Lindenb. (Lindner *et al.* 2004). As a result, eighteen species are currently known from Madagascar (Marline *et al.* 2012). Marline *et al.* (2020) listed three further species, but details were lacking and the vouchers are not accessible (T. A. J. Herrington pers. com.), therefore these new reports are not taken into account here.

In the framework of the MadBRYO project of the Natural History Museum of Paris and Missouri Botanical Garden (<https://www.madbryo.org/>), a taxonomic revision of the genus *Plagiochila* in Madagascar was made, taking into account the numerous new collections gathered in the last forty years, especially those of T. Pócs and his associates kept in herbarium EGR. The updated taxonomic treatment presented here may help improving our knowledge of the diversity and distribution of the genus *Plagiochila* in Madagascar.

## MATERIAL AND METHODS

The present account is based on study of the holdings of *Plagiochila* from Madagascar kept in the herbaria of Eszterházy Károly Catholic University, Eger (EGR), Meise Botanic

KEY TO SPECIES OF *PLAGIOCHILA* (DUMORT.) DUMORT. FROM MADAGASCAR

1. Ventral leaf margin undulate. Leaves ampliate, ventrad ..... 2
- Ventral leaf margin not undulate (or slightly undulate at the base only). Leaves ampliate or not ampliate, horizontally spreading or ventrad ..... 4
2. Ventral leaf base shortly and narrowly decurrent, the decurrent strip linear, less than 0.2 mm long, entire, not undulate. Underleaves absent. Ventral leaf margin undulate and sometimes with long and sharp teeth. Leaf cells 10-20 µm wide in midleaf, with large confluent trigones and strongly angular-undulate lumina ..... *P. rodriguezii* Steph.
- Ventral leaf base longly and broadly decurrent, the decurrent strip broadly lanceolate, more than 0.2 mm long, undulate and usually ciliate-laciniate. Underleaves present. Ventral leaf margin undulate, without long and sharp teeth. Leaf cells slightly larger, 18-25 µm wide in midleaf, trigones not confluent, lumina not strongly angular-undulate ..... 3
3. Ventral stem surface with paraphyllia between leaf bases, the paraphyllia very small, consisting of short rows of rounded cells. Ventral leaf margin undulate in the lower half ..... *P. squamulosa* Mitt.
- Ventral stem surface without paraphyllia. Ventral leaf margin usually undulate over its entire length ..... *P. corrugata* (Nees) Nees & Mont.
4. Some or all dorsal leaf bases toothed ..... 5
- Dorsal leaf bases entire ..... 6
5. Dorsal stem surface with paraphyllia (between the leaf bases). Leaves falcato-secund, subtransverse to obliquely spreading ..... *P. sikorae* Steph.
- Dorsal stem surface without paraphyllia. Leaves obliquely to widely spreading, not falcato-secund ..... *P. barteri* Mitt.
6. Leaves conspicuously falcate and strongly elongate, leaf apex with two very long, divaricate teeth. Leaf cells 1.5-2× longer than wide ..... *P. drepanophylla* Sande Lac.
- Leaves not conspicuously falcate and elongate, leaf apex bifid or not bifid. Leaf cells less elongate ..... 7
7. Stem leaves ± ampliate, 1-2-2.5× longer than wide ..... 8
- Stem leaves not ampliate, 2-3× longer than wide (when in doubt try both leads) ..... 15
8. Branch leaves suberect, stem leaves spreading outwards (obliquely). Stem leaves ± entire ..... *P. angusta* Lindenb.
- All leaves spreading outwards. Stem leaves usually toothed (± entire in *P. repanda* var. *repanda*) ..... 9
9. Leaf cells very large, 35-50 µm wide in midleaf. Plants robust, 5-9 mm wide. Rare species on Madagascar ..... 10
- Leaf cells smaller. Plants 2-5(-6) mm wide. Common species on Madagascar ..... 11
10. Leaves alternate. Teeth linear, small, 2-5 cells long, 1-2 cells wide at the base. All or part of the leaf cells at least papillose by small rounded papillae ..... *P. boryana* Steph.
- Leaves subopposite. Teeth triangular, large, 4-8 cells long, 3-6 cells wide at the base. All leaf cells smooth ..... *P. macrostachya* Lindenb.
11. Ventral leaf margin entire. Leaf apex entire or with a few small teeth (not bifid) ..... *P. repanda* (Schwägr.) Lindenb. var. *repanda*
- Ventral leaf margin toothed. Leaf apex toothed, sometimes bifid ..... 12
12. Leaves horizontally spreading. Trigones large and swollen, or small and not swollen. Cells in the dorsal leaf bases not elongate ..... 13
- Leaves ventrad. Trigones small, not or scarcely swollen. Cells in the dorsal leaf bases sometimes elongate ..... 14
13. Leaf cells rather small, 15-25 µm wide in midleaf (leaves not very transparent), trigones strongly swollen and becoming confluent at the leaf margin, margin cells usually thicker-walled. Leaf apex mostly bifid ..... *P. repanda* var. *perrotana* (Steph.) Vanden Bergh.
- Leaf cells larger, (20-)25-30 µm wide in midleaf (leaves more transparent), trigones not or hardly swollen, not confluent at the margin, margin cells not thicker-walled. Leaf apex bifid or not bifid ..... *P. incerta* Steph.

14. Leaves narrowly oblong, (1.5-)2-3× longer than wide, teeth on leaf margins often terminating in a very long, 2-4× longer than wide cell. Cells in the dorsal bases of stem leaves not conspicuously elongate ..... *P. terebrans* Lindenb.  
 — Leaves less elongate, 1.3-2× longer than wide, teeth terminating in a shorter cell. Cells in the dorsal bases of stem leaves often conspicuously elongate ..... *P. kiaeri* Gottsche
15. Terminal branches present (sometimes only few, in the upper part of the plant) ..... 16  
 — Terminal branches absent ..... 19
16. Leaf apex strongly bifid, the apical teeth to 15 cells long. Leaves horizontally spreading. Rare montane species ..... *P. vandenberghenii* Gradst., sp. nov.  
 — Leaf apex entire or toothed, not strongly bifid. Leaves ventrad or horizontally spreading ..... 17
17. Leaves ventrad. Plants irregularly pinnate in the lower part and dichotomous in the upper part (or purely pinnate). Underleaves absent. Common species in montane environments ..... *P. terebrans* Lindenb.  
 — Leaves horizontally spreading. Plants purely dichotomous. Underleaves present. Rare lowland species ..... 18
18. Leaf margins entire or with 1-4 short teeth (1-3 cells long) at apex. Leaf cells *c.* 15-20 µm wide in midleaf, thin-walled. In coastal rainforest, rare ..... *P. strictifolia* Steph.  
 — Apical and ventral leaf margin with 15-20 long teeth (3-10 cells long). Leaf cells larger, *c.* 25 µm wide in midleaf, ± thick-walled with radiate trigones. Occurrence on Madagascar to be confirmed ..... *P. boivini* Steph.
19. Leaves fragmenting, upper part of leaf frequently broken away ..... 20  
 — Leaves not fragmenting, but sometimes caducous ..... 21
20. Leaves horizontally spreading, narrowly oblong, 2-3× longer than wide, fragmenting near the apex. Leaf margins entire or with 2-4 blunt lobes at the apex ..... *P. fracta* Pócs  
 — Leaves subtransverse, 1.5-2× longer than wide, fragmenting in the lower half. Leaf margins with 4-7 sharp teeth in the upper half (teeth at apex largest) ..... *P. bifaria* (Sw.) Lindenb.
21. Mature stem leaves 2-3× longer than wide, narrowly oblong to ligulate to rectangular ... *P. pectinata* Lindenb.  
 — Mature stem leaves 1-2× longer than wide, suborbicular to (ob)ovate-oblong to ovate-rectangular [when in doubt try both leads] ..... 22
22. Caducous leaves present ..... 23  
 — Caducous leaves absent ..... 25
23. Leaves oblong, widest in the middle, 1.5-2× longer than wide. Trigones small, not bulging. Leaf base without vitta-like area of larger cells. Plants without leafless, stoloniform shoots. Perianth with a short stalk at the base ..... *P. simplex* (Sw.) Lindenb.  
 — Leaves obovate, widest above the middle, 1-1.5(-2)× longer than wide. Trigones of stem leaves large, bulging. Leaf base with a vitta-like area. Plants often with leafless, stoloniform shoots (due to caducous leaves). Perianth without stalk at the base ..... 24
24. Leaves 1-1.3× longer than wide, toothed at apex and along the ventral margin ..... *P. punctata* (Taylor) Taylor var. *punctata*  
 — Leaves more elongate, 1.3-2× longer than wide, entire or with a few small teeth at apex ..... *P. punctata* var. *paucidentata* (Mont. & Gottsche) Gradst., comb. nov.
25. Leaf apex bifid. Plants small, 1.5-2 mm wide. Lowland slender phenotype of ..... *P. repanda* var. *perrotana* (Steph.) Vanden Bergh.  
 — Leaf apex not bifid. Plants 2-5 mm wide. Lowland or montane ..... 26
26. Plants 2-3.5 mm wide. Leaves narrowed to the apex, toothed at the apex and along most of the ventral margin. Cuticle ± papillose. Leaf base with a vitta-like area of larger cells ..... *P. stricta* Lindenb.  
 — Plants larger, 4-5 mm wide. Leaves not narrowed to the apex (apex broadly rounded), with very small teeth near the apex. Cuticle smooth. Leaf base without vitta-like area ..... *P. integerrima* Steph.

Garden (BR), Muséum national d'Histoire naturelle, Paris (PC), University of Göttingen (GOET) and selected types, mostly from Geneva (G). In total about 350 collections were studied. Particular attention was paid to the rich collections in EGR (*c.* 140 specimens) made by Professor T. Pócs and his

associates in Madagascar in the years 1990, 1994, 1998 and 2004. The taxa accepted by Vanden Berghen (1981), Grolle (1995) and others were re-assessed based on the study of the specimens, new descriptions and illustrations were prepared, and a key to accepted taxa was constructed.

## RESULTS

Twenty two species of *Plagiochila* (including four varieties) are reported from Madagascar in this paper, in six sections:

1. *Plagiochila* sect. *Africanae* Heinrichs: *P. barteri* Mitt., *P. sikorae* Steph.;
2. *Plagiochila* sect. *Arrectae* Carl: *P. bifaria* (Sw.) Lindenb., *P. punctata* (Taylor) Taylor var. *punctata*, *P. punctata* var. *paucidentata* (Mont. & Gottsche) Gradst., comb. nov., *P. stricta* Lindenb.;
3. *Plagiochila* sect. *Cucullatae* Schifffn.: *P. integerrima* Steph.;
4. *Plagiochila* sect. *Heteromallae* Lindenb. (synonym: sect. *Rutilantes* Carl): *P. fracta* Pócs, *P. pectinata* Lindenb., *P. simplex* (Sw.) Lindenb.;
5. *Plagiochila* sect. *Hylacoetis* Carl: *P. boryana* Steph., *P. macrostachya* Lindenb.;
6. *Plagiochila* sect. *Vagae* Lindenb.: *P. angusta* Lindenb., *P. corrugata* (Nees) Nees & Mont., *P. drepanophylla* Sande Lac., *P. incerta* Gottsche, *P. kiaeri* Gottsche, *P. repanda* (Schwaegr.) Lindenb. var. *repanda*, *P. repanda* var. *perrotana* (Steph.) Vanden Bergh., *P. rodriguezii* Steph., *P. squamulosa* Mitt., *P. strictifolia* Steph., *P. terebrans* Lindenb., *P. vandenberghenii* Gradst., sp. nov.

Four species are newly recorded from Madagascar: *P. vandenberghenii* Gradst., sp. nov., *P. strictifolia* (previously known from West Africa), *P. bifaria* and *P. simplex*. The latter two are common and widespread in tropical America and are new to Africa; *P. bifaria* additionally occurs in western Europe. *Plagiochila simplex* had been recorded from Africa (La Réunion) by Lindenberg (1840), but this record is considered erroneous (Grolle 1995). In addition, the neotropical *P. macrostachya* is reported new to Africa based on the synonymy of *P. granditexta* Steph. The latter species was considered endemic to Madagascar but proved to be identical to *P. macrostachya*. Furthermore, *P. paucidentata* Mont. & Gottsche is reduced to varietal rank in *P. punctata* and *P. sikorae* is restored as a good species; the latter was considered a synonym of *P. barteri* by Vanden Berghen (1981) and later authors.

Among the liverwort genera of Madagascar, *Plagiochila* ranks fourth in terms of number of species, after *Cololejeunea* (54 spp.), *Frullania* (38) and *Diplasiolejeunea* (26) (Marline *et al.* 2012). About half of all the African species, estimated at about 40 (Heinrichs *et al.* 2005a), occur in Madagascar and at least three species are endemic to the island: *P. fracta*, *P. sikorae* and *P. vandenberghenii* Gradst., sp. nov. The high *Plagiochila* richness of Madagascar is undoubtedly due to the large ecodiversity of the country – even though only 10% of the original vegetation is remaining (Myers *et al.* 2000; Vences *et al.* 2009) – especially the large tracts of humid tropical montane forest, which are the preferred habitat of *Plagiochila*. The Madagassan *Plagiochila* floras is rather similar to that of La Réunion, but the latter island has slightly fewer species and has two taxa, *P. boivini* Steph. and *P. exigua* (Tayl.) Tayl. that are not yet known from Madagascar (even though *P. boivini* was reported from Madagascar by

Vanden Berghen 1981). These two species are expected to occur in Madagascar.

Based on their distribution, five main biogeographic patterns can be discerned among the *Plagiochila* species of Madagascar:

1. Endemic to Madagascar: *P. fracta*, *P. sikorae*, *P. vandenberghenii* Gradst., sp. nov.;
2. East African Islands: *P. angusta*, *P. incerta*, *P. punctata* var. *paucidentata* (Mont. & Gottsche) Gradst., comb. nov.;
3. East Africa: *P. drepanophylla*, *P. kiaeri*, *P. repanda*, *P. rodriguezii*, *P. squamulosa*;
4. Tropical Africa: *P. barteri*, *P. integerrima*, *P. pectinata*, *P. strictifolia*, *P. terebrans*;
5. Afro-American: *P. bifaria*, *P. boryana*, *P. corrugata*, *P. macrostachya*, *P. punctata*, *P. simplex*, *P. stricta*; two of them, *P. bifaria* and *P. punctata*, occur also in western Europe.

The data indicate that Madagascar is particularly rich in East African taxa; almost half of the recorded species (10) are mainly restricted to eastern Africa. A further noteworthy feature is the richness in Afro-American taxa, which include one third of all species found in Madagascar. Three of these are newly reported in this paper (*P. bifaria*, *P. macrostachya*, *P. simplex*). In contrast, none of the *Plagiochila* species from Madagascar occur in Asia. The absence of Asian taxa among the Madagassan *Plagiochilas* is unexpected since many tropical Asian bryophyte species have ranges extending to Africa (Pócs 1976, 1992). Their absence may perhaps be an artifact, reflecting a lack of comparison of the African and Asia *Plagiochila* floras.

Interestingly, more than half of the Afro-American species (*P. bifaria*, *P. macrostachya*, *P. simplex*, *P. stricta*) are unknown from the African mainland, having a “peri-Afro-American” range. Such ranges are explained by extinction of species on the mainland, due to the drying-out of the African continent during the Pleistocenic glaciations (Stearn 1971; Moore 1973). The occurrence of peri-Afro-American ranges in bryophytes was discussed by Gradstein *et al.* (1983) and Gradstein (2013). About twenty bryophyte species are known having this type of distribution and most of them occur in the understory of dense rainforest or mossy forests. The preference of these species for wet habitats coincides with their presumed extinction during the climatically dry periods of the Pleistocene (Gradstein 2013).

## SYSTEMATICS

Synonyms include species recorded from Madagascar. The specimens are arranged according to the six major provinces, as it is sometimes difficult or impossible to assign them to smaller regional units. Habitats of the species in Madagascar follow the regional vegetation classification of Moat & Smith (2007). Accordingly, the species of *Plagiochila* occur in humid or subhumid evergreen forests between 0–2130 m, including lowland forests (0–800 m), mid-elevation forests (800–1500 m), and montane forests and ericaceous bushes (>1500 m).

Phylum MARCHANTIOPHYTA  
Family PLAGIOCHILACEAE  
Genus *Plagiochila*

*Plagiochila angusta* Lindenb.  
(Fig. 1)

*Plagiochila angusta* Lindenb., *Species Hepathicarum* (fasc. 5): 148 (1843). — Type: France. La Réunion, *unknown collector*, ex hb. Lehmann (holo-, UPS; *vide* Grolle 1995).

*Plagiochila chenagona* Steph., *Bulletin de la Société royale de Botanique de Belgique* 31: 119 (1892). — Type: Madagascar (Vanden Berghen 1981; Grolle 1995).

*Plagiochila furcata* Steph., *Bulletin de la Société royale de Botanique de Belgique* 31: 120 (1892). — Type: Madagascar (Vanden Berghen 1981).

*Plagiochila pallida* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 340 (1882). — Type: Madagascar (Grolle 1995).

SPECIMENS EXAMINED. — Madagascar. Ambatovary forest, Imerina, *Camboué s.n.* (PC as *P. calva* det. Stephani; Dugas 1928). — Prov. Antananarivo • Mantasoa lake, III.1974, *Onraedt 70M8155* (BR), *70M2047* (BR as *P. angustitexta*); Mandraka Forest Reserve, II.1974, *Onraedt 70M2190* (BR); Ankazobe, Ambohitantely Reserve, IX.1994, *Pócs 9444/J*, *Pócs 9444/M*, *Pócs 9444/N* (EGR). — Prov. Antsiranana • Andasibe-Mantadia Nat. Park, III.1990, *Pócs et al. 90104/AM* (EGR as *P. repanda*); Amber Mountain Nat. Park, VIII.1973, *Cremers 2760* (BR as *P. furcata*); Manongarivo-Ambahatra Reserve, ridge of Ambahatra Mt., III.1999, *Geissler 19849/1* (EGR, G); Marojejy Nat. Park, Andampibe valley, III.1990, *Pócs 90112/J p.p.* (EGR). — Prov. Fianarantsoa • Andringitra Nat. Park, VII.1955, *Bosser 9629* (BR as *P. cambuena*, det. Vanden Berghen); ridge E of camp III, IX.1994, *Pócs 9474/G* (EGR); E of Korokoro river, *Pócs 9476/F* (EGR); Ranomafana Nat. Park, park gate near Ambodiamontana, VII.2004, *Pócs et al. 04118/AZ* (EGR, GOET), *04118/AW*, *04118/AX*, *04118/BA* (EGR); Sahamalaoatra Forest, near Vohipara, *Pócs et al. 04120/BV* (EGR, GOET), *04120/BS*, *04120/BY* (EGR); slope of Mt. Vatolampy, *Pócs 04129/J* (EGR); Sava, Makizovana massif, 420 m, *Reeb 213D*, *225* (PC). — Prov. Toamasina • near Andasibe (“Perinet”), c. 900 m, III.1974, *Cremers 3124*, *3126*, *3169* (BR as *P. furcata* and *P. angustitexta*); Andasibe-Mantadia Nat. Park, III.1990, *Pócs et al. 90104/AM* (EGR as *P. repanda*); S of Andasibe-Mantadia Nat. Park, summit of Mt. Maromizaha, VIII.1998, *Pócs 9890/BQ* (EGR).

ADDITIONAL SPECIMEN EXAMINED. — Madagascar. Without locality, *Forsyth Major 100*, syntype of *P. gentiliana* Steph. (G00068927; *vide* Grolle 1995).

DISTRIBUTION AND HABITAT. — East African Islands (Madagascar, La Réunion). In Madagascar found on bark (tree trunks, branches, twigs) in the understory of humid to subhumid mid-elevation forests, between 500-1500 m.

DESCRIPTION (see also Vanden Berghen 1981 as *Plagiochila chenagona*)

Plants 2-4 mm wide, to 10 cm long, long and slender, dichotomously branched, branches terminal, occasionally intercalary on broken stems, rhizome-like creeping shoot present. Leaves contiguous to imbricate, branch leaves suberect (spreading at angles of c. 15-30° with the stem), slightly ampliate, very asymmetrically ovate-oblong, to 0.5 mm long, c. 1.5-2× longer

than wide, apical margin with 3-5 teeth with the central tooth being largest, margins and bases otherwise entire; leaves towards stem bases more widely, obliquely spreading and distinctly ampliate, ovate-subrectangular with a broad rounded apex, c. 1.2-1.4× longer than wide, margins entire or with a few irregular, small teeth (up to 10); dorsal leaf bases shortly to longly decurrent, swollen, with elongate cells, not concealing the stem, ventral leaf bases shortly and very narrowly decurrent, decurrent ventral part to 0.2 mm long, entire. Leaf cells irregularly (sub)isodiametrical to slightly elongate in midleaf, c. 15-25 µm wide in midleaf, trigones rather small, cordate or slightly swollen, sometimes confluent, cells towards the leaf margin smaller, subrectangular, in basal stem leaves sometimes thicker-walled and forming a weak, yellowish, 1-3 cells wide, cells towards the swollen dorsal leaf base frequently elongate, rectangular, but not elongate towards the midbasal portion of the leaf, vitta-like region absent; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia intercalary, with 5-10 pairs of bracts. Perianth without stalk, perianth mouth conspicuously and longly lacinate. Vegetative reproduction not observed.

NOTES

*Plagiochila angusta* (sect. *Vagae* Lindenb.) is distinguished by the long and flaccid, mostly dichotomously branched plants (branching terminal) with suberect to obliquely spreading branch leaves with a few teeth at apex and more widely spreading, ampliate stem leaves with almost fully entire margins. The contrast between suberect, toothed branch leaves and more widely spreading, subentire stem leaves usually allows to recognize the species at a glance. However, populations may occur in which the difference between branch and stem leaves is not very pronounced (e.g. plants from Forêt d’Ambatovary collected by Camboué and identified by Stephani as *P. calva*). The leaf cells in *P. angusta* are rather small, c. 15-25 µm wide in midleaf, with small, cordate or slightly swollen trigones; the cells are sometimes conspicuously elongate towards the swollen dorsal base, but not towards the midbasal portion (vitta-like area absent); stem leaves of robust plants are sometimes bordered by small, thicker-walled cells in 1-3 rows.

The stem leaves of *P. angusta* may resemble those of *P. repanda*, but in the latter species they are more widely spreading and the trigones are much larger and strongly swollen. Moreover, branches of *P. repanda* are very few and mostly intercalary, very rarely terminal.

*Plagiochila barteri* Mitt.  
(Fig. 2)

*Plagiochila barteri* Mitt., *Journal of the Linnean Society, Botany* 22: 320 (1886). — Type: Sierra Leone. *Barter s.n.* (holo-, NY; *vide* Grolle 1995).

SPECIMENS EXAMINED. — Madagascar. “Mts. Morojezy”, 1300 m, *Guillaumet 4150* (PC). — Prov. Antsiranana • Manongarivo-Ambahatra Reserve, ridge of Ambahatra Mt., III.1999, *Geissler 19460/1* (EGR, G).

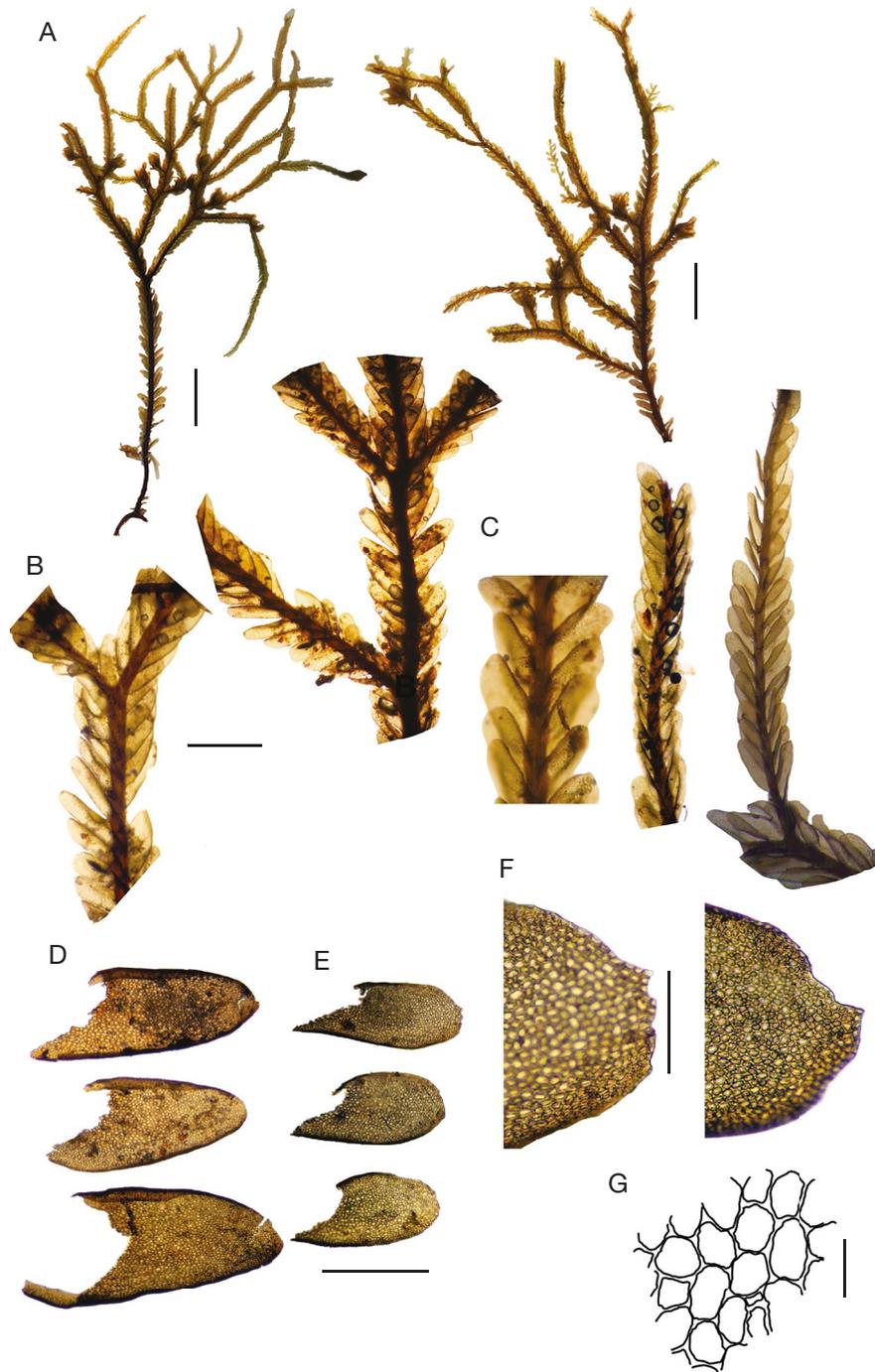


FIG. 1. — *Plagiochila angusta* Lindenb.: **A**, habit; **B**, shoots with terminal branches; **C**, branches; **D**, stem leaves; **E**, branch leaves; **F**, leaf apex; **G**, midleaf cells. From Reeb CR213D (PC). Scale bars: A, 5 mm; B-E, 1 mm; F, 0.25 mm; G, 0.025 mm.

**DISTRIBUTION AND HABITAT.** — Widespread in the mountains of tropical Africa. In Madagascar apparently rare, found twice on rotten wood in humid mid-elevation forest, 850-950 m. Further Madagassan records belong to *P. sikorae*.

**DESCRIPTION** (see also Jones 1962; Vanden Berghen 1981) Plants rather robust, 3-5 mm wide, to 10 cm long, unbranched or with a few short branches, all branches intercalary, rhizome-like creeping shoot present, dorsal stem surface without para-

phyllia. Mature stem leaves imbricate, obliquely to widely spreading, asymmetrically and narrowly elongate-triangular, *c.* 2-2.5× longer than wide, widest at the base, ampliate, the ventral bases forming a high crest, apex ± truncate, margins frequently bordered by thicker-walled cells, with 20-50 teeth, apex with 2-3 short teeth, ventral margin with 10-25 linear teeth, dorsal margin with 2-15 teeth and dorsal base with 2-8 teeth, the teeth 1-6 cells long and usually longest at the ventral leaf base, made up of quadrate to narrowly rectangular cells, the tip

cell strongly elongate; dorsal base longly and broadly decurrent, the decurrent part swollen concealing the stem, ventral base shortly and narrowly decurrent, the decurrent linear portion to 0.1 mm long. Leaf cells isodiametrical to somewhat elongate, 20–25 µm wide in midleaf, with large, trabeculate trigones, often more strongly thickened towards the leaf margin and forming a border, leaf base with a short vitta-like area, cells in the dorsal leaf base frequently elongate; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia terminal to intercalary. Perianth base covered by bracts, perianth mouth longly ciliate-laciniate. Vegetative reproduction by leaf fragmentation.

NOTES

*Plagiochila barteri* (sect. *Africanae* Heinrichs) is a robust species that is recognized by purely intercalary branching and wide-spreading, narrowly ovate-triangular leaves with toothed dorsal leaf bases and strongly ampliate ventral bases. The dorsal leaf bases are longly and broadly decurrent and ± concealing the stem, the leaf margins have 20–50 linear teeth with a strongly elongate tip cell, and the leaf cells are rather small, 20–25 µm wide in midleaf, with large trigones and sometimes forming a border of thicker-walled cells, and being elongate in the dorsal leaf base. A variety with subentire and rather short and broad, conspicuously bordered leaves, *P. barteri* var. *valida* (Steph.) Vanden Bergh. (lecto-, designated here: La Réunion, 1889, *Rodriguez* 38, G00068917!), occurs in the Mascarenes (Vanden Berghen 1981) and may be expected to occur in Madagascar.

*Plagiochila sikorae* Steph. was treated as a synonym of *P. barteri* by Vanden Berghen (1981) but is here restored as a good species, differing from *P. barteri* in the presence of paraphyllia on the dorsal stem surface and ± falcato-secund leaves with fewer teeth (less than 20). Most specimens from Madagascar cited in Vanden Berghen (1981) under the name *P. barteri* belong to *P. sikorae*.

*Plagiochila bifaria* (Sw.) Lindenb.  
(Fig. 3)

*Jungermannia bifaria* Sw., *Nova Genera et Species Plantarum seu Prodrromus*: 145 (1788). — *Plagiochila bifaria* (Sw.) Lindenb., *Species Hepathicarum* (fasc. 5): 127 (1843). — Type: **Jamaica**. Swartz *s.n.* (holo-, S!).

ADDITIONAL SPECIMENS EXAMINED. — **Madagascar**. **Prov. Antananarivo** • Ankaratra, Manjakatempo Forest Reserve, saddle between Mt. Andriandra and Mt. Ambohimandrana, on soil in montane forest mixed with *Plagiochila terebrans*, 2050–2130 m, IX.1994, *Pöcs* 9481/AA (EGR, GOET).

DISTRIBUTION AND HABITAT. — Peri-Afro-American (tropical America, Madagascar) and western Europe; new to Africa. In Madagascar found in a mossy montane forest at 2050–2130 m.

DESCRIPTION (see also Heinrichs *et al.* 1998, 2004a; Paton 1999 as *Plagiochila killarniensis* Pearson)

Plants 2–3 mm wide, to 4 cm long, irregularly pinnate, all branches intercalary. Creeping, rhizome-like primary stem not

observed. Mature stem leaves distant to contiguous, obliquely spreading and strongly ventrad to subtransverse, subfalcate, asymmetrically obovate-oblong, 1.5–2× longer than wide, widest in or above the middle, the upper half or two third often broken away, ventral leaf base not ampliate and not shouldered, apex rounded to truncate, margins unbordered, dorsal margin straight or slightly curved, narrowly recurved, ventral margin arched, leaves with 4–7 widely-spatiated teeth at apex and on the upper half of the ventral margin, two teeth at apex being larger than the other ones, the apex appearing asymmetrically bifid, teeth narrowly to broadly triangular, 2–6(–15) cells long, sometimes broken, made up of subquadrate cells, the tip cell more elongate; leaf bases shortly and narrowly decurrent, the decurrent ventral portion 0.15–0.3 mm long. Leaf cells subisodiametrical to somewhat elongate, 20–30 µm wide in midleaf, 1–1.5× longer than wide, with rather small, well-defined, swollen trigones, the trigones usually not radiate, intermediate thickenings occasionally present, leaf base with a conspicuous vitta-like area of larger and wider cells; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia terminal to intercalary, with 3–5 pairs of bracts. Perianth campanulate, exerted beyond the bracts, mouth coarsely toothed, base without stalk. Vegetative reproduction by leaf fragmentation.

NOTES

*Plagiochila bifaria* (sect. *Arrectae* Carl) is a widely distributed and highly variable neotropical-western European species that is for the first time recorded from Africa. Characteristic are the fragmenting, subtransverse, obliquely spreading, obovate-oblong leaves with several teeth in the upper half including two larger apical ones (up to 15 cells long), the leaves thus appearing bifid, and the presence of a distinct vitta-like area of larger cells at the leaf base (Heinrichs *et al.* 1998, 2004a). The species differs from *P. punctata*, another member of the sect. *Arrectae* in Madagascar, by having fragmenting instead of caducous leaves. The Madagassan *P. bifaria* plants stand out by having rather few teeth per leaf (4–7) and were growing mixed with *P. terebrans*, but clearly differed from the latter species by the darker brown color and subtransverse, less elongate leaves with an asymmetrically bifid apex.

*Plagiochila boryana* Steph.  
(Fig. 4)

*Plagiochila boryana* Steph., *Bulletin de la Société royale de Botanique de Belgique* 31 (2): 118 (1892). — Type: **France**. La Réunion, *Rodriguez* 174 (lecto-, designated by Heinrichs [2002], G00064121; isolecto-, PC0785962!).

ADDITIONAL SPECIMEN EXAMINED. — **Madagascar**. **Prov. Fianarantsoa** • Andringitra Mts. Nat. Park, montane rainforest along tributary W of Korokoro river, 1000–1270 m, IX.1994, *Pöcs* 9473/AZ (EGR).

DISTRIBUTION AND HABITAT. — Afro-American: at high elevation in East Africa (Uganda, Tanzania) and on La Réunion and Madagascar, furthermore occurring in the mountains of southeastern Brazil and Bolivia where it was described as *Plagiochila guttulata* Herzog (Heinrichs 2002). *Plagiochila boryana* was recorded from Madagascar

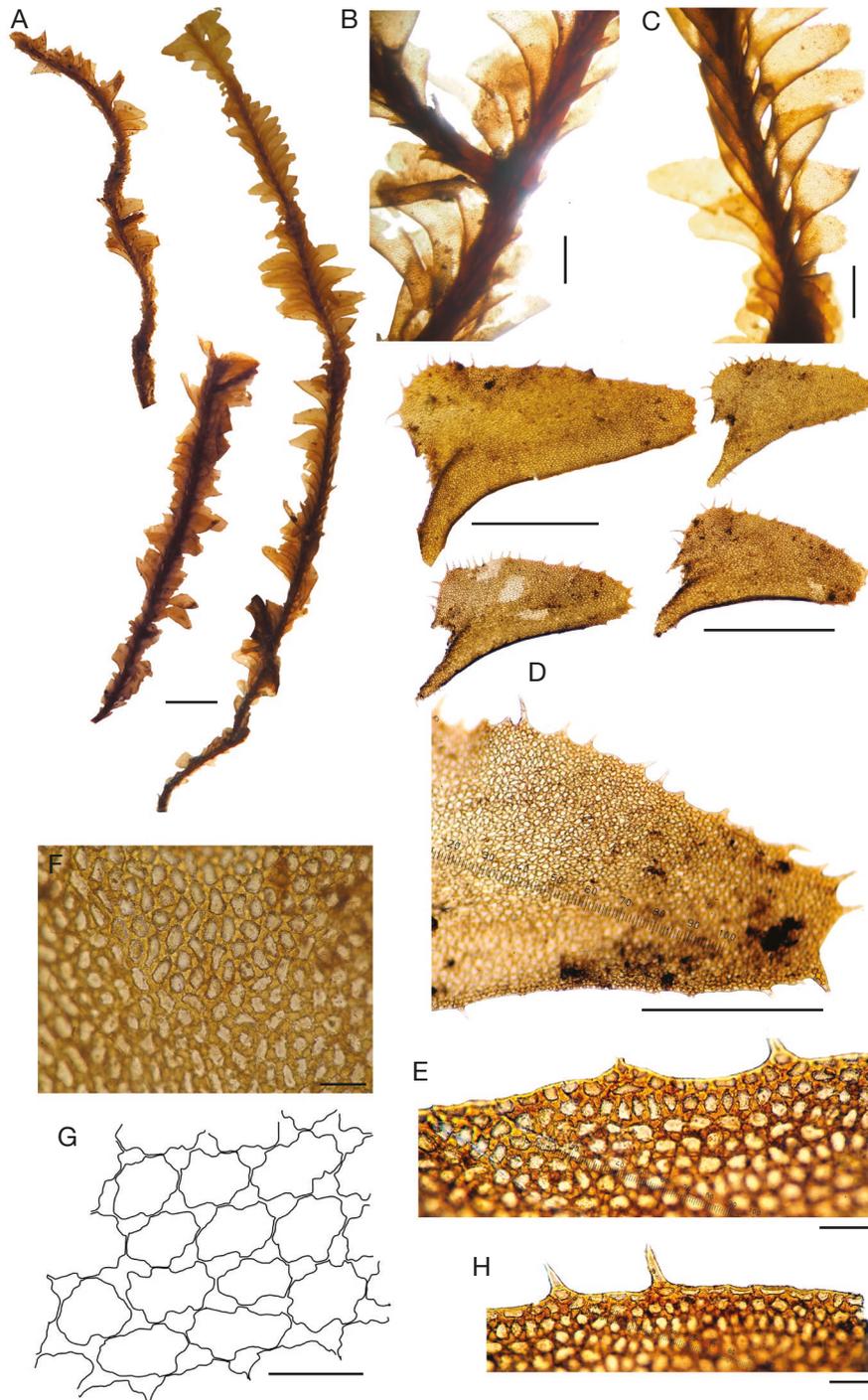


FIG. 2. — *Plagiochila barteri* Mitt.: **A**, habit; **B**, shoot with intercalary branch; **C**, shoot in dorsal view; **D**, leaves, showing the presence of teeth at the dorsal leaf base; **E**, upper part of leaf; **F**, **G**, midleaf cells; **H**, leaf margin. From Geissler 19460 (EGR). Scale bars: A, 2 mm; B, C, E, H, 0.5 mm; D, 1 mm; F, 0.05 mm; G, 0.025 mm.

by Stephani (1892b, 1893), but this record was not mentioned in Vanden Berghen (1981) and Heinrichs (2002); the occurrence of *P. boryana* on Madagascar is here confirmed. The species was found in Madagascar on twigs in subhumid mid-elevation forest, 1000-1270 m.

**DESCRIPTION** (see also Vanden Berghen 1981; Heinrichs 2002)

Plants robust, 5-9 mm wide, little branched, all branches intercalary, rhizome-like creeping shoot present. Mature

stem leaves loosely imbricate, widely spreading, alternate, ovate-oblong to ovate-triangular, *c.* 1.5× longer than wide, widest at the base, ampliate, unbordered, apex rounded, margins with 10-25(-50) teeth, the teeth rather short, 2-5 cells long, mostly linear with a 1-2 cell wide base, present at the apex, along the ventral margin and, occasionally, at the dorsal base; dorsal base longly decurrent, the decurrent part partly covering the stem, ventral base rather shortly and narrowly decurrent. Leaf cells isodiametrical to somewhat elongate,



FIG. 3. — *Plagiochila bifaria* (Sw.) Lindenb.: **A**, habit; **B**, dry shoots in lateral view; **C**, shoots in dorsal view; **D**, shoot in ventral view; **E**, intercalary branches (leaves removed); **F**, leaves; **G**, leaf apex; **H**, leaf base; **I**, **J**, midleaf cells. From Pócs 9487 (EGR). Scale bars: A-C, F, 1 mm; D, E, 0.5 mm; G, H, 0.25 mm; I, J, 0.05 mm.



FIG. 4. — *Plagiochila boryana* Steph.: **A**, habit; **B**, intercalary branching; **C**, shoot in dorsal view; **D**, **E**, shoot in ventral view, showing amplate leaf bases; **F**, leaves; **G**, leaf margin with teeth; **H**, **I**, midleaf cells, showing papillose cuticle. From Bolivia, *Heinrichs 4353, 4104* (GOET) and Réunion, *Bizot 2985* (PC). Scale bars: A, 5 mm; B, 0.5 mm; C-F, 1 mm; G, 0.1 mm; H, I, 0.05 mm.

very large, 35–45 µm wide in midleaf, with small trigones, leaf base without vitta-like area; cuticle densely papillose to almost smooth, the papillae numerous per cell, rounded to oblong; oil bodies not observed. Underleaves absent. Male plants slightly smaller than female plants. Androecia in a cluster of 3–5 male branches at the stem apex. Perianth without stalk, perianth mouth with numerous narrowly triangular or linear teeth. Vegetative reproduction absent.

#### NOTES

*Plagiochila boryana* (sect. *Hylacoetis* Carl) is recognized by the robust plants (more than 5 mm wide) with purely intercalary branching, ampliate leaves with rather short, linear teeth (2–5 cells long, 1–2 cells wide at the base), very large leaf cells (35–45 µm wide in midleaf) and a papillose cuticle. The papillosity of the cuticle varies and in the Madagassan collection (*Pócs 9473/AZ*) part of the leaf cells were smooth. The dorsal leaf bases in the species are normally entire (Heinrichs 2002) but Vanden Berghen (1981) observed toothed dorsal leaf bases in robust populations from the African mainland.

By its large leaf cells *P. boryana* differs from all Madagassan *Plagiochila* species except the rare *P. macrostachya* (synonym: *P. granditexta*). The latter species is readily separated from *P. boryana* by its subopposite leaves, coarser triangular teeth and fully smooth cuticle.

#### *Plagiochila corrugata* (Nees) Nees & Mont. (Fig. 5)

*Jungermannia corrugata* Nees, *Flora Brasiliensis seu Enumeratio Plantarum* 1 (1): 378 (1833). — *Plagiochila corrugata* (Nees) Nees & Mont., *Annales des Sciences naturelles, Botanique* (sér. 2) 5: 52 (1836). — Type: **Brazil**. *Martius s.n.* (holo-, STR; *fide* Heinrichs *et al.* 2004b).

*Plagiochila cambuena* Steph., *Botanical Gazette* 15: 289 (1890) — Type: **Madagascar** (Vanden Berghen 1981; Heinrichs *et al.* 2004b).

*Plagiochila madagascariensis* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4 (6): 594 (1904), *nom. illeg.* — Type: **Madagascar** (Vanden Berghen 1981).

*Plagiochila undulata* Dugas, *Annales des Sciences naturelles, Botanique* (sér. 10) 11: 121, 188 (1928), *nom. illeg.* — Type: **Madagascar** (Grolle 1995).

**SPECIMENS EXAMINED.** — **Madagascar.** Plateau de Ikanga, *Besson 326* (PC). — **Prov. Antsiranana** • Marojejy Reserve, Mandena, III.1990, *Pócs et al. 90110/A* (EGR as *P. repanda*, GOET). — **Prov. Antananarivo** • Bonjolava Forest, IX.1974, *Cremers 3444* (BR); Lake Mantasoa, VIII.1959, *Bosser 13122* (BR); III.1974, *Onraedt 70M2171* (BR); VII.1998, *Pócs et al. 9851/A* (EGR); Mandraka Forest, *Onraedt 70M2176, 70M2193* (BR). — **Prov. Fianarantsoa** • Ambositra, Amalateray, on trees, 1800 m, *Onraedt 70M0396* (EGR as *P. rodriguezii*); Andringitra Nat. Park, VII.1955, *Bosser 9632* (BR); Pic Bobby, IX.1994, *Vojtkó 9458/H, 9458/W* (EGR); tributary W of Korokoro river, *Pócs 9473/AV* (EGR); Ifanadiana, Ranomafana village, VII.2004, *Pócs 04122/B* (EGR); Ranomafana Nat. Park, Namorona river waterfalls, VII.2004, *Pócs 04126/AS* (EGR); slope of Mt. Vatolampy near Ambatolahy village, *Pócs 04129/AB* (EGR, GOET), *04129/AC, 04129/H* (EGR).

**DISTRIBUTION AND HABITAT.** — Afro-American: in Africa largely restricted to East Africa, in tropical America occurring in southern subtropical regions (southeastern Brazil, northern Argentina, Paraguay, Bolivia). Its distribution resembles that of *P. boryana*. In Madagascar *P. corrugata* is found on bark and rock in humid to subhumid evergreen forests and coffee plantations, from sea level to 2000 m.

**DESCRIPTION** (see also Vanden Berghen 1981 as *P. cambuena*; Heinrichs *et al.* 2004b)

Plants 2–4 mm wide, to 8 cm long, rigid, irregularly pinnate, dichotomous in younger parts, branching terminal and intercalary. Creeping, rhizome-like shoot present, short. Stem surface without paraphyllia (but teeth on the decurrent ventral leaf bases and on underleaves may sometimes resemble paraphyllia). Mature stem leaves imbricate and ventrad, obliquely spreading and somewhat curved outwards, very asymmetrical, ovate-triangular, 1–1.5× longer than wide, ampliate, ventral margin strongly undulate-crispate over most of its length but without teeth except at the base (in plants from Madagascar), apex entire or with a few short teeth, dorsal margin narrowly recurved, entire; dorsal bases longly and broadly decurrent, concealing the stem, ventral base longly and broadly decurrent, usually more than 0.2 mm long, undulate and with a few cilia and lacinia. Leaf cells subisodiametrical, *c.* 18–25 µm wide in midleaf, rather thin-walled, with small cordate to slightly swollen trigones; vitta-like area absent; cuticle smooth; oil bodies not observed. Underleaves present, up to 0.5 mm long, deeply bifid, outer margins often with cilia or lacinia. Androecia terminal to intercalary, of 4–10 pairs of bracts. Perianth without stalk, perianth mouth densely toothed by shortly triangular teeth. Vegetative reproduction by cladia from ventral leaf surfaces.

#### NOTES

*Plagiochila corrugata* (sect. *Vagae*) is recognized by the rigid, irregularly (bi)pinnate to dichotomous plants with terminal and intercalary branches, and with ampliate, ventrad leaves with strongly undulate-crispate ventral margins and longly and broadly decurrent bases, which are concealing the stem surface. Underleaves are present. By the undulate-crispate ventral leaf margins *P. corrugata* is similar to *P. squamulosa* and *P. rodriguezii*, but *P. rodriguezii* differs in the shortly and narrowly decurrent ventral leaf bases without cilia or lacinia on the decurrent strip, absence of underleaves, and smaller leaf cells (10–20 µm wide in midleaf) with large trigones and angular-undulate lumina. *Plagiochila squamulosa*, a common and variable species in the mountains of East Africa (Jones 1962; Vanden Berghen 1981) that is very rare in Madagascar, is more closely similar to *P. corrugata*, but differs by numerous small paraphyllia on the ventral stem surface. The paraphyllia can be confused with underleaves and lacinia of ventral leaf bases, but differ from the latter by the rounded cells of the paraphyllia, those of amphigastria and lacinia being quadrate to elongate.

Vanden Berghen (1981) noted a close morphological similarity between *P. corrugata* (synonym: *P. cambuena*) and *P. ulata* Inoue & Grolle from New Guinea. However, the latter species has undulate dorsal leaf margins (Piippo 1989); in *P. corrugata* the dorsal leaf margins are plane.

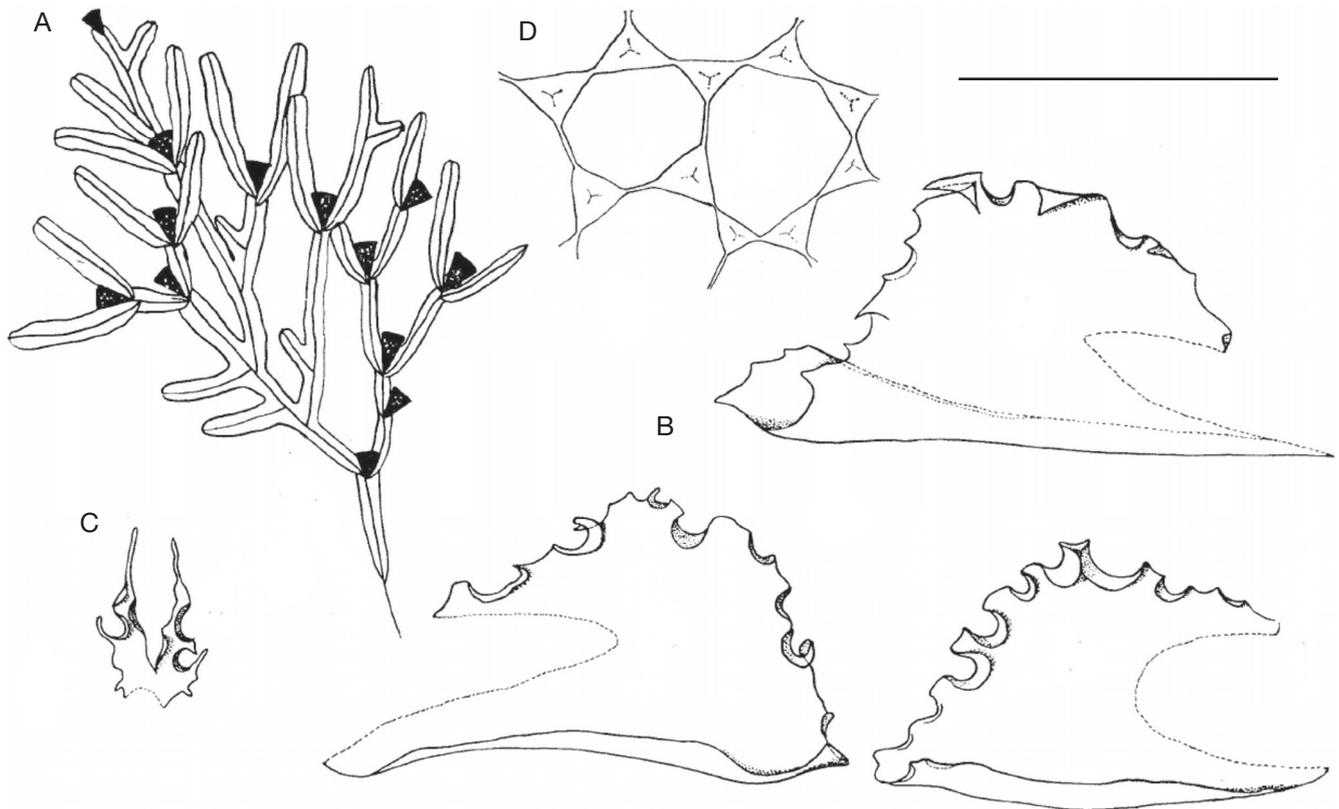


FIG. 5. — *Plagiobhila corrugata* (Nees) Nees & Mont.: **A**, habit; **B**, leaves; **C**, underleaf; **D**, midleaf cells. Redrawn from Vanden Berghen (1981).

*Plagiobhila drepanophylla* Sande Lac.

(Fig. 6)

*Plagiobhila drepanophylla* Sande Lac., *Synopsis Hepaticarum Javanicarum*: 103 (1857). — Type: **France**. La Réunion, *unknown collector* (holo-, L; *fide* Vanden Berghen 1981).

*Plagiobhila dicrana* Mitt., *Journal and Proceedings of the Linnean Society of London* 22: 320 (1886). — Type: **Madagascar** (Grolle 1995).

**SPECIMENS EXAMINED.** — **Madagascar**. **Prov. Antsiranana** • Marojejy Nat. Park, elfin forest on ridge, 1000-1400 m, III.1990, *Pócs 90114/BJ* (EGR). — **Prov. Antananarivo** • Lake Mantasoa, III.1974, *Onraedt 70M2116* (BR); IV.1986, *Tixier 8234* (BR); Angavokely, near Carion, I.1970, *Onraedt 70M82* (BR). — **Prov. Fianarantsoa** • c. 33-34 km S of Ambositra, c. 1650 m, VIII.1871, *Onraedt 70M5380, 70M5324a* (BR); IX.1994, *Pócs 9479/E* (EGR); Ankazonivady Forest Reserve, 16 km S of Ivato, VII.2004, *Pócs et al. 04115/Q* (EGR); Ramomafana Nat. Park, W slope of Mt. Vatolampy, VII.2004, *Pócs 04129/F* (EGR); summit ridge of Mt. Vatolampy, *Pócs 04128/F* (EGR); beyond park boundary, Mt. Namatoana, *Pócs & Tuba 04130/AQ* (EGR); between Fianarantsoa and Mananjary, *Besson s.n.*, isosyntype of *Plagiobhila valida* Steph. (PC0103073!). — **Prov. Toamasina** • near Moramanga, X.1994, *Pócs 9489* (EGR, GOET); Andasibe-Mantadia Nat. Park, Mt. Andrianavibe, X.1994, *Pócs 9487/BV, 9487/CJ* (EGR).

**DISTRIBUTION AND HABITAT.** — East Africa (Tanzania), Madagascar, La Réunion. In Madagascar found on bark in humid or subhumid mid-elevation and montane forests, 900-2000 m.

**DESCRIPTION** (see also Jones 1962; Vanden Berghen 1981) Plants 2.5-4.5 mm wide, to 5 cm long, dichotomous or slightly and irregularly pinnate, branching terminal and intercalary, rhizome-like creeping shoot present. Mature stem leaves contiguous to subimbricate, suberect in the lower half, widely and horizontally spreading in the upper half, very asymmetrical, narrowly triangular-falcate, c. 2-3× longer than wide, widest near the base, ampliate, the ampliate ventral leaf bases sometimes forming an undulate crest that is concealing the stem; branch leaves less ampliate; leaf margins unbordered (but cells sometimes slightly more elongate-rectangular towards leaf margin), apex usually bifid, with (1-)2 very long, lobe-like teeth (to 0.3 mm long), the apical teeth erect to widely diverging (divariacate), ventral margin entire or with a few linear to narrowly triangular teeth (1-7), dorsal margin without or with one small tooth near apex, ventral and dorsal bases entire, dorsal bases longly and rather broadly decurrent, concealing the stem, ventral base conspicuously and very narrowly decurrent, the linear decurrent portion to 0.2 mm long, entire. Leaf cells c. 15-20 μm wide in midleaf, subrectangular, 1.5-2× longer than wide, the cells with conspicuous trigones, trigones cordate to swollen and slightly trabeculate; vitta-like area absent; cuticle smooth; oil bodies not observed. Underleaves present, very small, deeply bifid. Androecia terminal to intercalary, of 3-6 pairs of bracts. Perianth without stalk, perianth mouth densely ciliate. Vegetative reproduction by regenerants from leaf surfaces (Vanden Berghen 1981).

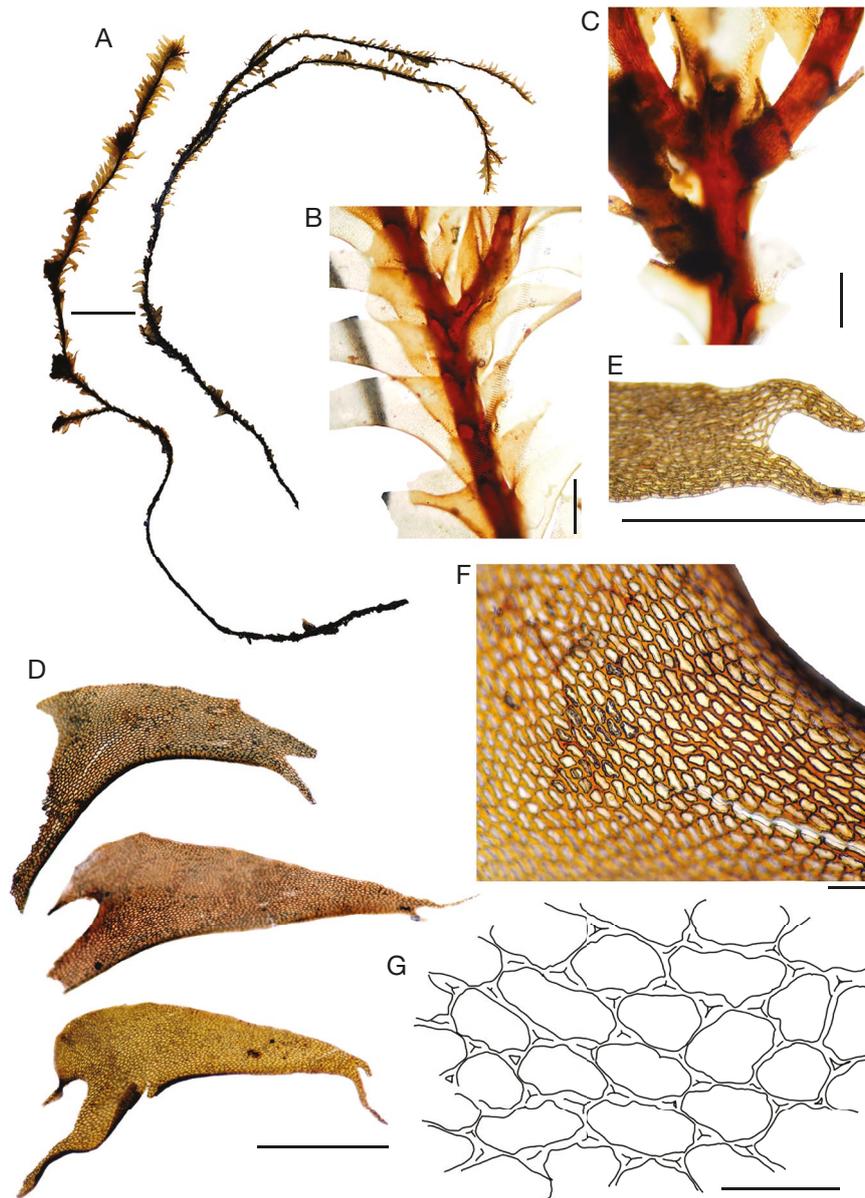


FIG. 6. — *Plagiochila drepanophylla* Sande Lac.: **A**, habit; **B**, shoot in dorsal view, with terminal branch; **C**, shoot with intercalary branches; **D**, leaves; **E**, leaf apex; **F**, midleaf cells and leaf margin; **G**, midleaf cells. From Pócs 9477 (EGR). Scale bars: A, 5 mm; B, C, E, 0.5 mm; D, 1 mm; F, G, 0.05 mm.

NOTES

*Plagiochila drepanophylla* (sect. *Vagae*) is readily recognized by the conspicuously falcate, asymmetrically bifid leaves with two large, sometimes widely, divaricately spreading teeth, longly decurrent dorsal and ventral leaf bases. Branching is terminal and intercalary. In the elongate leaf cells and conspicuously bifid apex, the species approaches members of the neotropical section *Fuscolutea*, especially *P. aerea* and *P. tabinensis*. The relationships of this species to other members of sect. *Vagae*, where Heinrichs *et al.* (2005a) place the species, are unclear and need study.

The isosyntype material in PC of *P. valida* Steph. (synonym: *P. barteri* var. *valida* [Steph.] VandenBergh.) from Madagascar, *Besson s.n.*, is a poorly preserved specimen of *P. drepanophylla*.

*Plagiochila fracta* Pócs  
(Fig. 7)

*Plagiochila fracta* Pócs, *Phytotaxa* 195 (2): 183 (2015). — Type: Madagascar. Prov. Antsiranana, Manongarivo-Ambahatra Reserve, on ridge between the two branches of Mt. Ambahatra, c. 800 m, on rock in montane forest, 1250-1300 m, III.1999, *Geissler19691/1* (holo-, G00281722; iso-, EGR; *vide* Pócs 2015).

DISTRIBUTION AND HABITAT. — Only known from the type from Madagascar.

DESCRIPTION (after Pócs 2015)

Plants very small, 0.8-1.3 mm wide, to 1 cm long, very flaccid, irregularly branched, branches intercalary, rhizome-like creeping shoot present. Mature stem leaves contiguous, rather

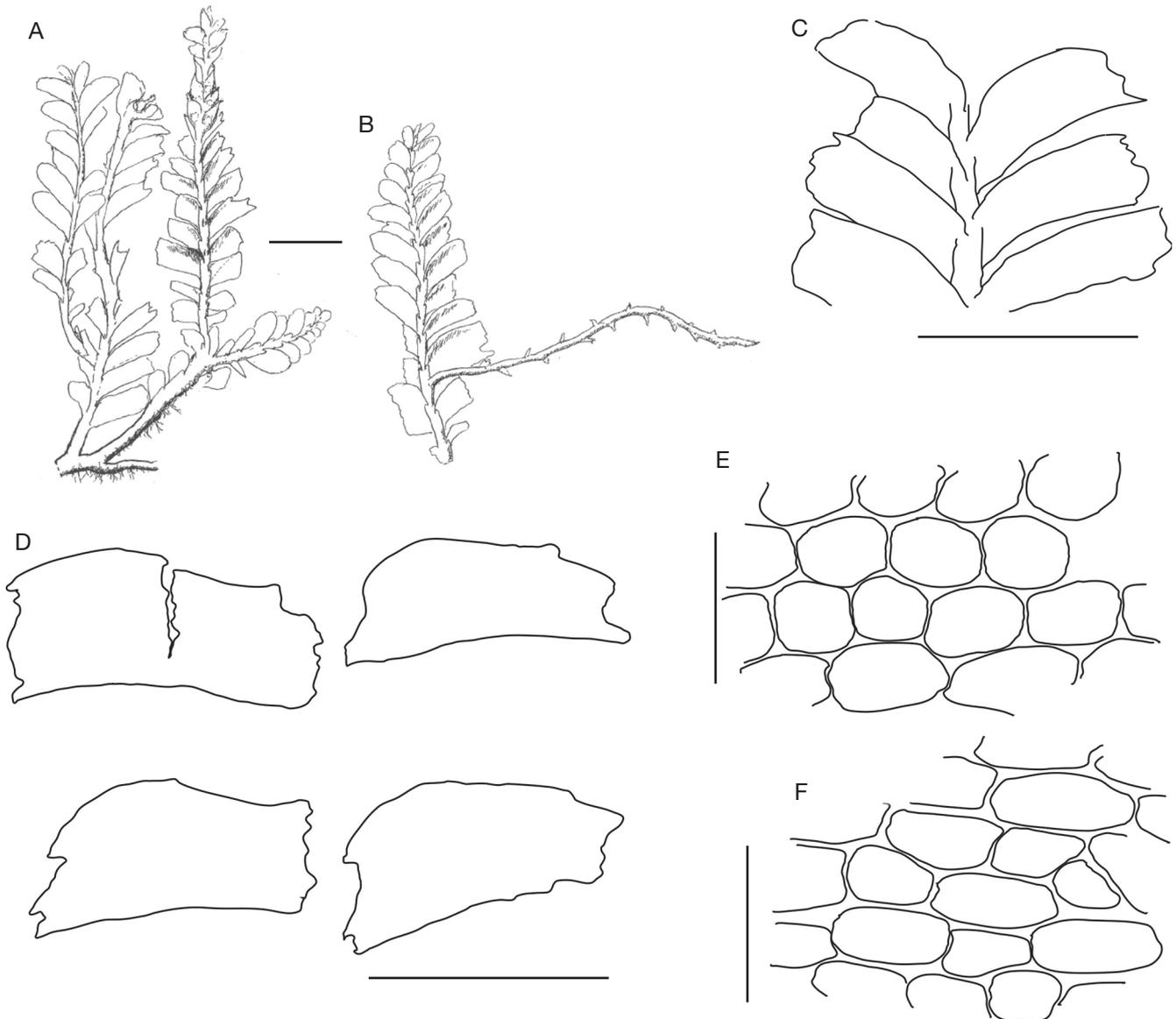


FIG. 7. — *Plagiobila fracta* Pócs: **A**, habit in dorsal view; **B**, habit in ventral view; **C**, detail of habit in ventral view; **D**, leaves; **E**, midleaf cells; **F**, basal leaf cells. Adapted from Pócs (2015). Scale bars: A, B, 1 mm; C, D, 0.5 mm; E, F, 0.05 mm.

widely and horizontally spreading, slightly asymmetrically oblong-ligulate, *c.* 2–3× longer than wide, widest in the middle, very fragile, irregularly fragmenting in the upper half, base not ampliate and not shouldered, apex rounded or 2–4 lobulate, without teeth; leaf bases shortly and narrowly decurrent. Leaf cells somewhat elongate, *c.* 15–2 μm wide in midleaf, with small trigones; leaf base without vitta-like area; cuticle smooth; oil bodies probably granular. Underleaves minute. Androecia slender, terminal to intercalary, with 3–5 pairs of bracts. Perianth campanulate, without stalk, perianth mouth laciniate. Vegetative reproduction by leaf fragmentation.

#### NOTES

*Plagiobila fracta* (sect. *Heteromallae* Lindenb.) is recognized by the very small plants with intercalary branching and horizontally spreading, oblong-ligulate, entire or shallowly 2–4

lobed leaves that are strongly fragmenting in the upper half (Pócs 2015). The species may be related to *P. pectinata*, but the latter is a larger plant with ventrad, toothed leaves that are caducous, not fragmenting.

#### *Plagiobila incerta* Gottsche (Fig. 8)

*Plagiobila incerta* Gottsche, *Annales des Sciences naturelles, Botanique* (sér. 4) 8: 324 (1857). — Type: **Mauritius**. *Comerson* 33 (lecto-, designated here, PC0100688!; isolecto-, G00064456!).

*Plagiobila crollii* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4(4): 356 (1904). — Type: **Madagascar**. 18.XI.1900, *Croll s.n.* (lecto-, designated by Grolle [1995], G00045461!).

*Plagiochila nemophila* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 339 (1882). — Type: Madagascar. “Silva Amabaranavaranututa”, 6.XII.1877, *Rutenberg s.n.* (lecto-, designated by Grolle [1995], G00128913!).

*Plagiochila boivinii* sensu Vanden Berghen (1981), non typus (*vide* Grolle 1995).

ADDITIONAL SPECIMENS EXAMINED. — Madagascar. NE Madagascar, *Pervillé s.n.* (PC). — Prov. Antananarivo • Mandraka Forest Reserve, II.1974, *Onraedt 74M 2172, 74M 2174, 74M 2175*, det. Vanden Berghen as *P. boivinii* (BR); I.1959, *Bosser 12580*, det. Vanden Berghen as *P. boivinii* (BR). — Prov. Antsiranana • Marojejy Reserve, Andampibe valley, III.1990, *Pócs 90112/f p.p.* (EGR). — Prov. Fianarantsoa • Vohiparara, III.1978, *Tixier 11543*, det. Vanden Berghen as *P. boivinii* (BR); Ranomafana Nat. Park, Sahamalaotra Forest near Vohipara village, VII.2004, *Pócs et al. 04120/BU* (EGR); Namorona river waterfalls, *Pócs 04126/CS* (EGR, GOET); slope of Mt. Vatolampy near Ambatolahy village, *Pócs 04129/G* (EGR); 1016 m. on pole, IX.2017, *Reeb17M619* (PC). — Prov. Toamasina • Masoala Peninsula W coast, summit ridge S of Amanizana village, among *Thysananthus spathulistipus*, IX.1994, *Pócs 9449/I* (EGR, GOET); Nosy Mangabe Island, *Pócs 9450/S* (EGR); Andasibe-Mantadia Nat. Park, III.1990, *Pócs et al. 90103/S, 90105/g, 90106/AA, 90106/P* (EGR); ridge of Mt. Andrianavibe, *Pócs 9487/BR, 9487/BX* (EGR).

DISTRIBUTION AND HABITAT. — East African Islands (Comores, Madagascar, La Réunion, Mauritius). In Madagascar found on bark in lowland and lower montane forests, from sea level to 1250 m. On La Réunion found at low elevation, 200–300 m (Vanden Berghen 1981).

DESCRIPTION (see also Vanden Berghen 1981 as *P. boivinii*) Plants 2.5–6 mm wide, to 8 cm long, flaccid, dichotomous or slightly and irregularly pinnate, branches usually intercalary, occasionally terminal, rhizome-like creeping shoot present. Mature stem leaves imbricate, widely and horizontally spreading, asymmetrically ovate-rectangular to narrowly ovate-triangular, 1.7–2× longer than wide, widest at the base, unbordered, ventral bases ampliate and forming a low crest, apex usually bifid, ventral margin plane or slightly undulate at the base, apex usually bifid, with two lobe-like teeth up to ten cells long and usually a smaller tooth in the middle, ventral margin toothed over almost its whole length with 10–20 narrowly triangular to linear teeth, the teeth 2–5(–10) cells long, made up of subrectangular cells; dorsal base long and broadly decurrent, covering part of the stem and made up of mostly short cells (rarely elongate), ventral bases shortly to rather longly and narrowly decurrent, the decurrent linear portion 0.1–0.4 mm long, entire. Leaf cells subisodiametrical, 20–35 µm wide in midleaf, with conspicuous but not or only slightly swollen trigones, leaf base without vitta-like area, cells in the dorsal leaf base not elongate; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia terminal. short, of 4–6 pairs of bracts. Perianth without stalk, perianth mouth densely laciniate. Vegetative reproduction not observed.

#### NOTES

*Plagiochila incerta* (sect. *Vagae*) is recognized by the rather robust plants with ampliate, horizontally spreading and regularly imbricate, ovate-triangular leaves with a toothed

and sometimes bifid apex, toothed ventral margin and entire or toothed ventral base, entire and longly and broadly decurrent dorsal leaf bases, and leaf cells with conspicuous but not strongly swollen trigones. Branching is terminal and intercalary. *Plagiochila incerta* may be confused with *P. repanda* var. *perrotana* and *P. kiaeri*, but *P. repanda* var. *perrotana* has leaves with smaller cells and large, swollen trigones and an ill-defined border of thicker-walled cells, whereas *P. kiaeri* differs by ventrad leaves with smaller cells and dorsal leaf bases with elongate cells.

Vanden Berghen (1981) provided a detailed description and illustrations of *P. incerta* under the name *P. boivinii* Steph. The type of *P. boivinii*, however, has non-ampliate leaves and small trigones, and is close to *P. africana* Steph. and *P. neckeroidea* Mitt. (see also Jones 1962). The confusion was apparently caused by the isolectotype material of *P. boivinii* (G00065447), which consists of a mixture of *P. boivinii* and *P. incerta* (Grolle 1995: 112). Our study of material in BR identified by Vanden Berghen as *P. boivinii* confirms that the material belongs to *P. incerta*.

Vanden Berghen (1981) suggested a close relationship between *P. incerta* (as “*P. boivinii*”) and the neotropical *P. montagnei*, but the latter species has underleaves (absent in *P. incerta*) and frequent vegetative reproduction by propagula from leaf surfaces (not observed in *P. incerta*). Moreover, the leaves in *P. montagnei* are more ovate-rectangular in shape and the leaf cells are smaller, 16–25 µm wide in midleaf, with small trigones (Heinrichs & Gradstein 2000).

#### *Plagiochila integerrima* Steph.

(Fig. 9)

*Plagiochila integerrima* Steph., *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 8: 83 (1886). — Type: São Tomé. *Moller 40* (holo-, G00045484; *vide* Grolle 1995).

*Plagiochila dichotoma* (P.Beauv.) Nees & Mont. var. *laxa* Gottsche *et al.*, *Synopsis Hepaticarum*: 35 (1844). — Type: Madagascar (Grolle 1995).

*Plagiochila radicans* Steph., *Bulletin de l’Herbier Boissier* (sér. 2) 2 (12): 971 (1902). — Type: Madagascar (Grolle 1995).

SPECIMENS EXAMINED. — Madagascar. Prov. Fianarantsoa • Andringitra Nat. Park, tributary W of Korokoro river, on streambed rocks, 750–1000 m, IX.1994, *Szabó 9472/S* (EGR). — Prov. Toamasina • W coast of Masoala Peninsula, S of Ambanizana village, on bark, 0–30 m, IX.1994, *Kis 9446/HG* (EGR). Furthermore recorded from Joffreville, Prov. Antsiranana (*Onraedt 70M5426*) and La Mandraka, Prov. Antananarivo (*Tixier 11205*) by Vanden Berghen (1981).

DISTRIBUTION AND HABITAT. — Widespread in tropical Africa. In Madagascar found on bark and rock in humid to subhumid lowland and mid-elevation forests, from sea level to 1000 m.

DESCRIPTION (see also Jones 1962; Vanden Berghen 1981; Müller *et al.* 1999; Fischer 2013)

Plants 3.5–5 mm wide, to 5 cm long, very flat, sparsely branched, branches intercalary. Creeping, rhizome-like



FIG. 8. — *Plagiochila incerta* Steph.: **A**, habit; **B**, shoot in ventral view with terminal female branch; **C**, shoot in dorsal view with intercalary branching; **D**, leaves; **E**, portion of leaf margin; **F**, **G**, leaf apex; **H**, **I**, midleaf cells. From Reeb CR17M619 (PC, TAN). Scale bars: A, 5 mm; B-D, 1 mm; E, 0.25 mm; F, G, 0.1 mm; H, I, 0.05 mm.

primary stem present. Mature stem leaves distant to subimbricate, ± widely and horizontally spreading, not ventrad, subsymmetrically oblong-obovate, *c.* 1.2-1.8× longer than wide, not ampliate, unbordered, apex very broad (about as broad as the leaf base), leaf not narrowed to the apex, rounded to truncate to emarginate, dorsal margin entire, with 5-20 short, triangular teeth in the upper half (like in *P. alternans*), most teeth at the apex, the teeth 1-4 cells long; dorsal and ventral bases scarcely decurrent, ventral base shortly recurved. Leaf cells subisodiametrical, 20-28 µm wide in midleaf, very thin-walled, trigones absent or minute, vitta-like area absent; cuticle smooth; oil bodies not seen. Underleaves present, very small. Gametocia not observed. Vegetative reproduction not observed.

NOTES

*Plagiochila integerrima* (sect. *Cucullatae* Schiffn.) is recognized by the obovate-oblong, non-ampliate, somewhat distant leaves with a very broad, rounded to truncate apex and small teeth in the upper half, scarcely decurrent leaf bases and very thin-walled leaf cells, without or with minute trigones.

*Plagiochila kiaeri* Gottsche  
(Fig. 10)

*Plagiochila kiaeri* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 341 (1882). — Type: **Madagascar**. *Borgen s.n.*, hb. Kiaer 1a (lecto-, designated by Grolle [1995], O).

*Plagiochila ankefinensis* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4 (2): 162 (1904). — Type: **Madagascar** (Vanden Berghen 1981).

*Plagiochila divergens* Steph., *Hedwigia* 30: 268 (1891). — Type: **Tanzania** (Jones 1962; Grolle 1995).

*Plagiochila evansii* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4 (4): 354 (1904). — Type: **Madagascar** (Grolle 1995).

*Plagiochila imerensis* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4 (6): 589 (1904). — Type: **Madagascar** (Vanden Berghen 1981).

*Plagiochila sparsa* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4 (2): 157 (1904). — *Plagiochila divergens* var. *sparsa* [Steph.] Vanden Berghen, *Bulletin du Jardin botanique national de Belgique* 51: 117 (1981). — Type: **Madagascar** (Vanden Berghen 1981).

SPECIMENS EXAMINED. — **Madagascar**. **Prov. Antananarivo** • Ankaratra, Manjakatempo Forest Reserve, VIII.1971, *Cremers 1701* (BR); Andramasina, *Tixier 8490* (PC). — **Prov. Antsiranana** • Marojejy Nat. Park, ridge N of Andampibe falls, III.1990, *Pócs 90113* (EGR). — **Prov. Fianarantsoa** • Ambatofitorahana 35 km S of Ambositra, I.1970, *Onraedt 70M426, 70M435* (BR); VIII.1971, *Onraedt 70M5322, 70M5382, 70M5739* (BR); near Ambositra, I.1970, *Onraedt 70M349, 70M349* (BR); Ambohimahasoa region N of Fianarantsoa, I.1970, *Onraedt 70M524, 70M525, 70M557* (BR); Andringitra Nat. Park, Pic Boby, IX.1994, *Vojtkó 9458/B* (EGR); Mt. Vohipia, *Pócs 9470/H* (EGR); Ankazonivady Forest Reserve, 16 km S of Ivato, VII.2004, *Pócs et al. 04115/A* (EGR, GOET), *04115/AA, 04115/Z* (EGR); Ranomafana Nat. Park, Sahamalaoatra Forest, VII.2004, *Pócs et al. 04120/BZ* (EGR). — **Prov. Toamasina** • Andasibe-Mantadia Nat. Park, Mt. Andrianavibe, X.1994, *Pócs 9487/BS* (EGR).

DISTRIBUTION AND HABITAT. — East Africa and Madagascar. In Madagascar on bark, rock and soil in subhumid mid-elevation forests, at 700-1800 m elevation.

DESCRIPTION (see also Vanden Berghen 1981 as *P. divergens*)

Plants 2-4 mm wide, to 6 cm long, long and slender, dichotomous in the upper part, irregularly pinnate below, branches mostly terminal, occasionally intercalary on broken stems, rhizome-like creeping shoot present. Leaves (sub)imbricate, obliquely spreading and ventrad, ± ampliate (more conspicuously ampliate towards the stem base), asymmetrically ovate-triangular, 1.3-2× longer than wide, irregularly toothed at apex and along the distal half of the ventral margin with 2-20(-25) rather small teeth, ventral leaf margin sometimes entire, apex sometimes bifid by two larger teeth, cells of the teeth short, 1-1.5(-2)× longer than wide, the tip cell of the teeth often broken, leaf margins and bases otherwise entire; dorsal leaf bases conspicuously swollen, shortly decurrent, partly concealing the stem, ventral leaf bases shortly and very narrowly decurrent, decurrent ventral part 0.1-0.2 mm long, entire. Leaf cells irregularly (sub)isodiametrical to slightly elongate, small, 12-20 µm wide in midleaf, trigones rather small, cordate or swollen, sometimes confluent, cells towards the leaf margin smaller, subrectangular, in basal stem leaves sometimes thicker-walled and forming a weak, yellowish, 1-3 cells wide border, cells towards the swollen dorsal leaf bases often conspicuously elongate, rectangular, but vitta-like region absent; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia intercalary, with 4-7 pairs of bracts. Perianth without stalk, perianth mouth densely ciliate-laciniate. Vegetative reproduction not observed.

NOTES

*Plagiochila kiaeri* (sect. *Vagae*) is recognized by the irregularly pinnate to dichotomous plants with or without terminal branching, leaves ± imbricate, ventrad, ovate-triangular and less than 2× longer than wide, ventral leaf margin and apex irregularly toothed with (0-)2-20(-25) triangular teeth made up of rather short cells (tip cell of teeth often broken), and with small leaf cells, only 12-20 µm wide in midleaf and usually elongate in the dorsal leaf bases, with rather small trigones. *Plagiochila kiaeri* may be confused with *P. incerta* and *P. terebrans*. *Plagiochila incerta* differs by the horizontally spreading leaves with larger cells (20-30 µm wide in midleaf) and cells in the dorsal leaf bases not elongate. For differences with *P. terebrans* see the key.

*Plagiochila macrostachya* Lindenb.  
(Fig. 11)

*Plagiochila macrostachya* Lindenb., *Species Hepathicarum* (fasc. 2-4): 75 (1840). — Type: **Jamaica**. Hb. Hooker (lecto-, designated by Heinrichs [2002], *W-Lindenb.* 66).

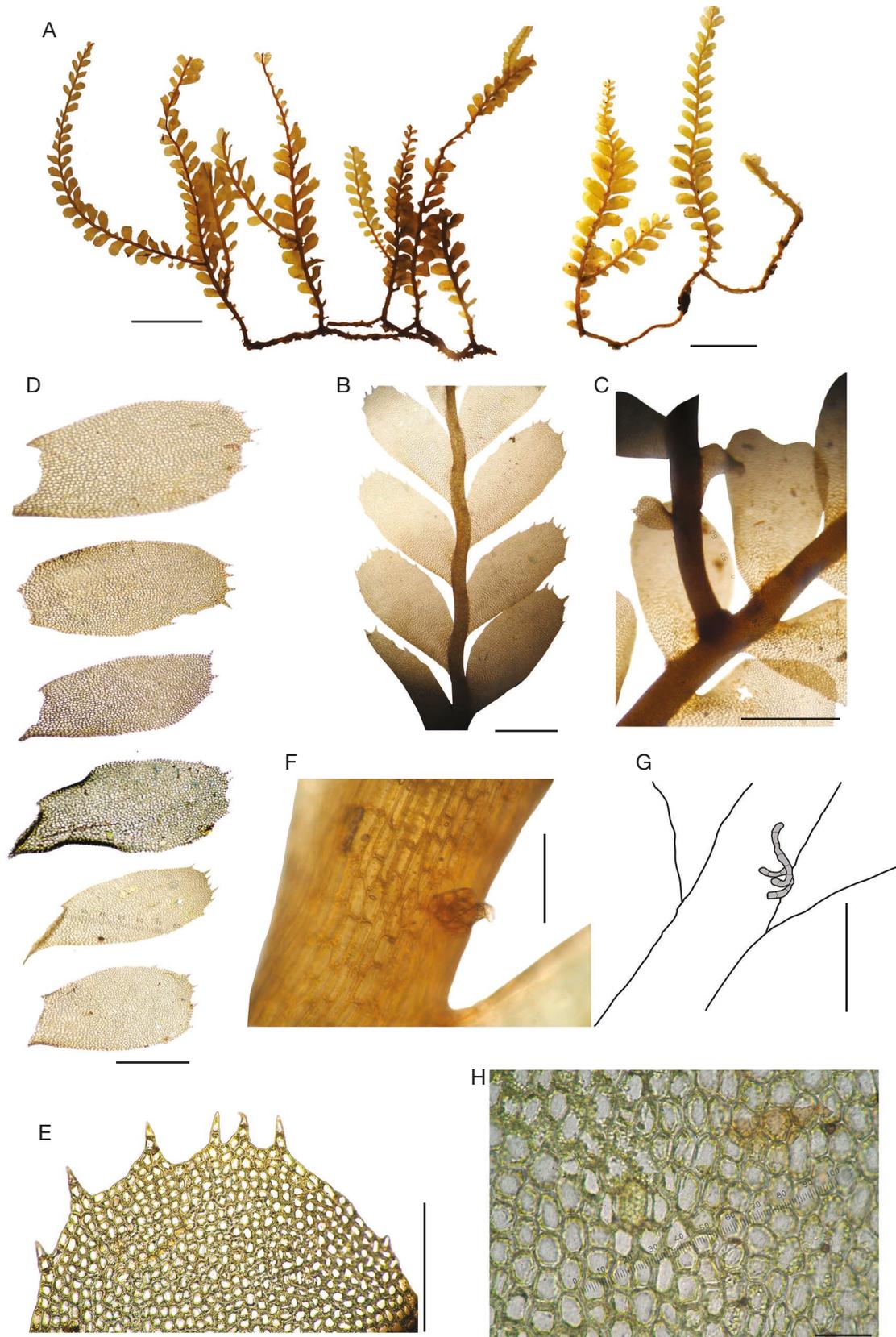


FIG. 9. — *Plagiobila integerrima* Steph.: **A**, habit; **B**, shoot in dorsal view; **C**, shoot with intercalary branch; **D**, leaves; **E**, leaf apex; **F**, **G**, underleaves; **H**, midleaf cells. From Szabo 9472/S (EGR). Scale bars: A, 5 mm; B-D, 1 mm; E, F, 0.1 mm; G, 0.25 mm; H, 0.05 mm.

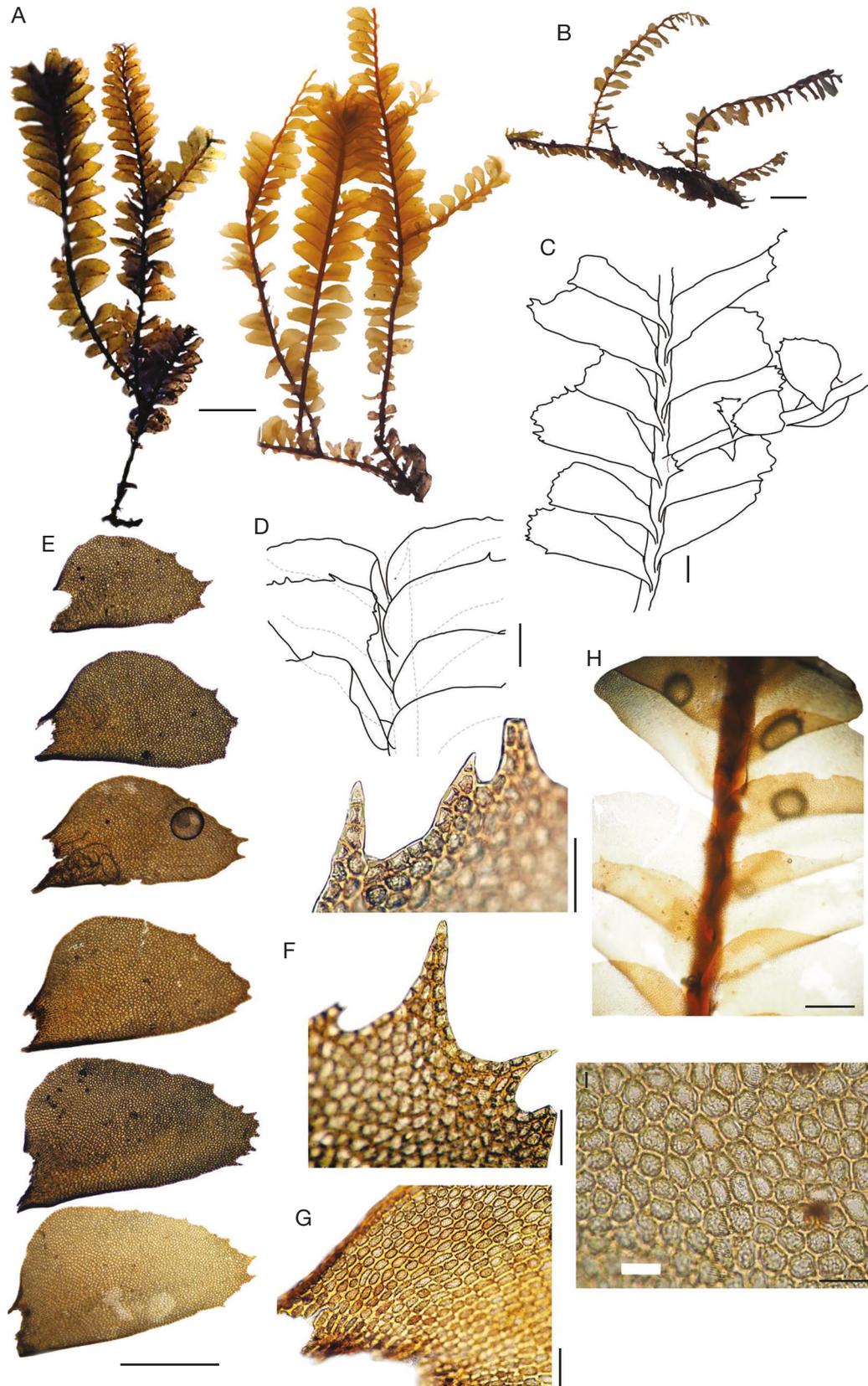


FIG. 10. — *Plagiochila kiaeri* Gottsche: **A**, habit; **B**, dry shoot in lateral view; **C**, shoot with intercalary branch in dorsal view; **D**, ampliate ventral leaf bases; **E**, leaves; **F**, portion of leaf margin, showing teeth; **G**, dorsal leaf base, showing elongate cells; **H**, shoot in ventral view showing ampliate leaf bases; **I**, midleaf cells. From Pócs 90113 (EGR). Scale bars: A, 5 mm; B, 2 mm; C, D, H, 0.5 mm; E, 1 mm; F, G, 0.1 mm; I, 0.05 mm.

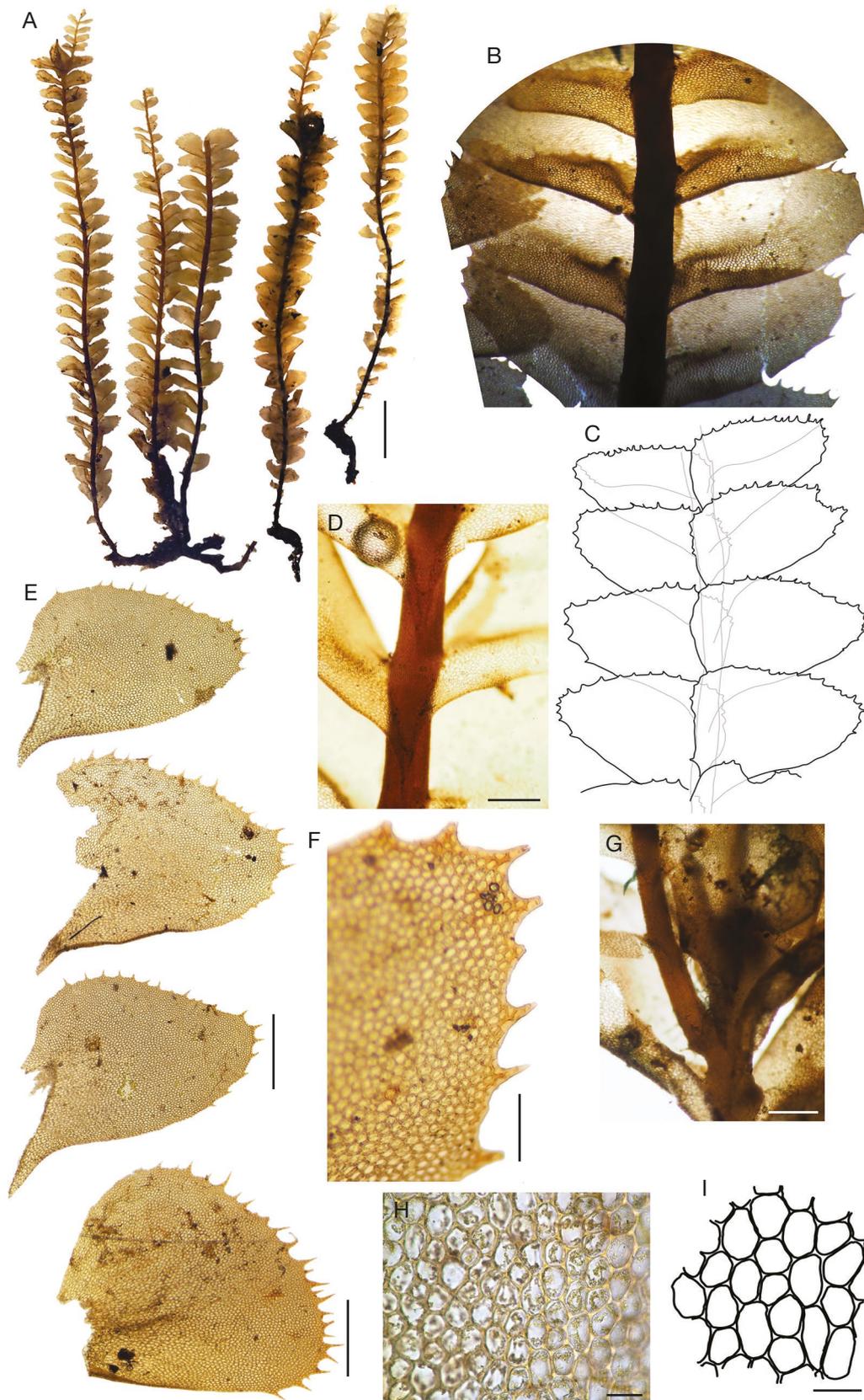


FIG. 11. — *Plagiochila macrostachya* Lindenb.: A, habit; B, C, shoot in ventral view, showing ampliate leaf bases; D, shoot in dorsal view; E, leaves; F, upper portion of leaf; G, intercalary branching; H, I, midleaf cells. From Bolivia, *Churchill 23663* (GOET). Scale bars: A, 5 mm; B, C, E, 1 mm; D, G, 0.5 mm; F, 0.25 mm; H, I, 0.05 mm.

*Plagiochila granditexta* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4 (2): 165 (1904) **syn. nov.** — Type: **Madagascar**. Unknown locality, *Hildebrandt s.n.* (holo-, G00045478!).

**DISTRIBUTION AND HABITAT.** — Peri-Afro-American: common throughout the mountains of tropical America (Heinrichs 2002), very rare in Madagascar; new to Africa. Previously recorded from La Réunion but the record belongs to *P. boryana* according to Grolle (1995).

**DESCRIPTION** (see also Vanden Berghen 1981 as *P. granditexta*; Heinrichs 2002)

Plants robust, *c.* 5 mm wide, vegetative branches scarce, all branches intercalary, rhizome-like creeping shoot present. Mature stem leaves loosely imbricate, widely spreading, subopposite, ovate-oblong to ovate-triangular, *c.* 1.5-2× longer than wide, widest at the base, ventral base with a high shoulder and ampliate on stem leaves, apex rounded, margins unbordered, with (5-)10-18 coarse triangular teeth along the apical and ventral margin, the teeth (3-)4-8 cells long, 3-6 cells wide at the base, sometimes broken; dorsal and ventral bases rather shortly and narrowly decurrent, the opposite bases almost connate. Leaf cells somewhat elongate, large, 35-40 µm wide in midleaf, trigones medium-sized, triangular-radiate with concave sides, vitta-like area absent; cuticle smooth; oil bodies not observed. Underleaves absent. Male plants not seen. Female bracts larger and more coarsely toothed than vegetative leaves. Perianth (juvenile) without stalk, perianth mouth with numerous triangular teeth. Vegetative reproduction not observed.

**NOTES**

*Plagiochila macrostachya* (sect. *Hylacoetis*) is recognized by the robust plants (at least 5 mm wide) with intercalary branching, subopposite leaves with a shoulder and distinctly ampliate in basal stem leaves, triangular teeth, large leaf cells (35-40 µm wide in midleaf) and a smooth cuticle. The species resembles *P. boryana* in the large leaf cells but in the latter species the leaves are alternate, the teeth linear and the cuticle papillose. The plants from Madagascar were described by Stephani as *P. granditexta* Steph., which is identical to *P. macrostachya* in all respects. Vanden Berghen (1981) erroneously illustrated the leaves of *P. granditexta* as being alternate.

*Plagiochila pectinata* Lindenb.  
(Fig. 12)

*Plagiochila pectinata* Lindenb., *Species Hepathicarum* (fasc. 1): 14 (1839). — Type: **Mauritius**. *Unknown collector* (holo-, W; *fide* Grolle 1995).

**SPECIMENS EXAMINED.** — **Madagascar**. **Prov. Antananarivo** • Ankaratra, Manjakatempo Forest Reserve, VIII.1971, *Cremers 1713, 1734* (BR); IX.1994, *Pócs 9481/AK, 9481/N* (EGR, GOET); Tavolotara Forest Reserve, XII.2017, *Reeb 17M904* (PC). — **Prov. Antsiranana** • Marojejy Nat. Park, XI.1972, *Guillaumet 4077, 4080* (BR); ridge N of Andampibe Falls, III.1990, *Pócs et al. 90113/CQ, 90113/CT, 90113/P* (EGR); elfin forest on ridge, *Pócs 90114/AN, 90114/BG* (EGR). — **Prov. Fianarantsoa** • Analabé near Ambositra,

VIII.1971, *Onraedt 71M5232, 71.M5236* (BR); Nosiarivo, X.1976, *Tixier 9464, 9465* (BR); Andringitra Nat. Park, tributary W of Korokoro river, IX.1994, *Pócs 9473/AY* (EGR, GOET); foot of Mt. Vohipia, *Pócs 9477/AN* (EGR); Ranomafana Nat. Park, ridge of Mt. Vohipanani, VII.2004, *Pócs 04121/DN* (EGR); summit ridge Mt. Vatolampy, *Pócs 04128/G* (EGR).

**DISTRIBUTION AND HABITAT.** — Widespread in tropical and southern Africa. In Madagascar commonly found on bark, rock, soil and rotten wood in subhumid to humid mid-elevation and montane forests, 700-2150 m.

**DESCRIPTION** (see also Jones 1962; Vanden Berghen 1981) Plants 3-5 mm wide, to 5 cm long, very flaccid, irregularly pinnate, branches intercalary, rhizome-like creeping shoot present. Mature stem leaves distant to contiguous, obliquely to widely spreading, somewhat ventrad, sometimes curved backwards, symmetrically or asymmetrically oblong-ligulate, *c.* 2-3× longer than wide, widest in the middle, often caducous, base not ampliate and not shouldered, leaves with 2-8 small to rather long triangular teeth at the apex and along the upper half of the ventral margin, the teeth 2-5-8) cells long, largest at the apex, made up of subquadrate cells, dorsal margin and leaf bases entire; leaf bases shortly and narrowly decurrent, decurrent ventral part *c.* 0.2 mm long. Leaf cells subrectangular, 20-30 µm wide in midleaf, 1.3-2× longer than wide, with conspicuous trigones, the trigones radiate on the longer cell walls and becoming confluent, margin cells sometimes thicker-walled and forming an obscure border; leaf base without vitta-like area; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia slender, terminal to intercalary, with 3-15 pairs of bracts, the bracts dorsally overlapping, ventrally not overlapping. Perianth obovate-oblong to subcylindrical, enveloped by bracts, not stalked, perianth mouth toothed by numerous coarse triangular teeth. Vegetative reproduction by caducous leaves.

**NOTES**

*Plagiochila pectinata* (sect. *Heteromallae*) is recognized by the wide-spreading, somewhat ventrad, narrowly oblong leaves, which are *c.* 2-3× as long as wide and toothed only in the upper part, and absence of terminal branches. The leaf cells are (sub)rectangular, 1.3-2× longer than wide, and sometimes thicker-walled along the leaf margin, forming an obscure border. *Plagiochila pectinata* may be confused with *P. terebrans* but the latter species has terminal branching and less strongly ventrad leaves, and the leaves are not caducous. *Plagiochila pectinata* approaches the neotropical *P. gymnocalycina* and *P. simplex*, but the leaves in the latter two species are less widely spreading and usually more strongly asymmetrical, with the ventral margin more widely arched outwards. Moreover, the leaf cells in *P. gymnocalycina* and *P. simplex* are less elongate, the leaf margins are not bordered by thicker-walled cells, and the perianth is elevated on a short stalk. In *P. pectinata* the perianth is not stalked. In *P. simplex*, moreover, the stem leaves are less than 2× longer than wide (more than 2× longer than wide in *P. pectinata* and *P. gymnocalycina*).

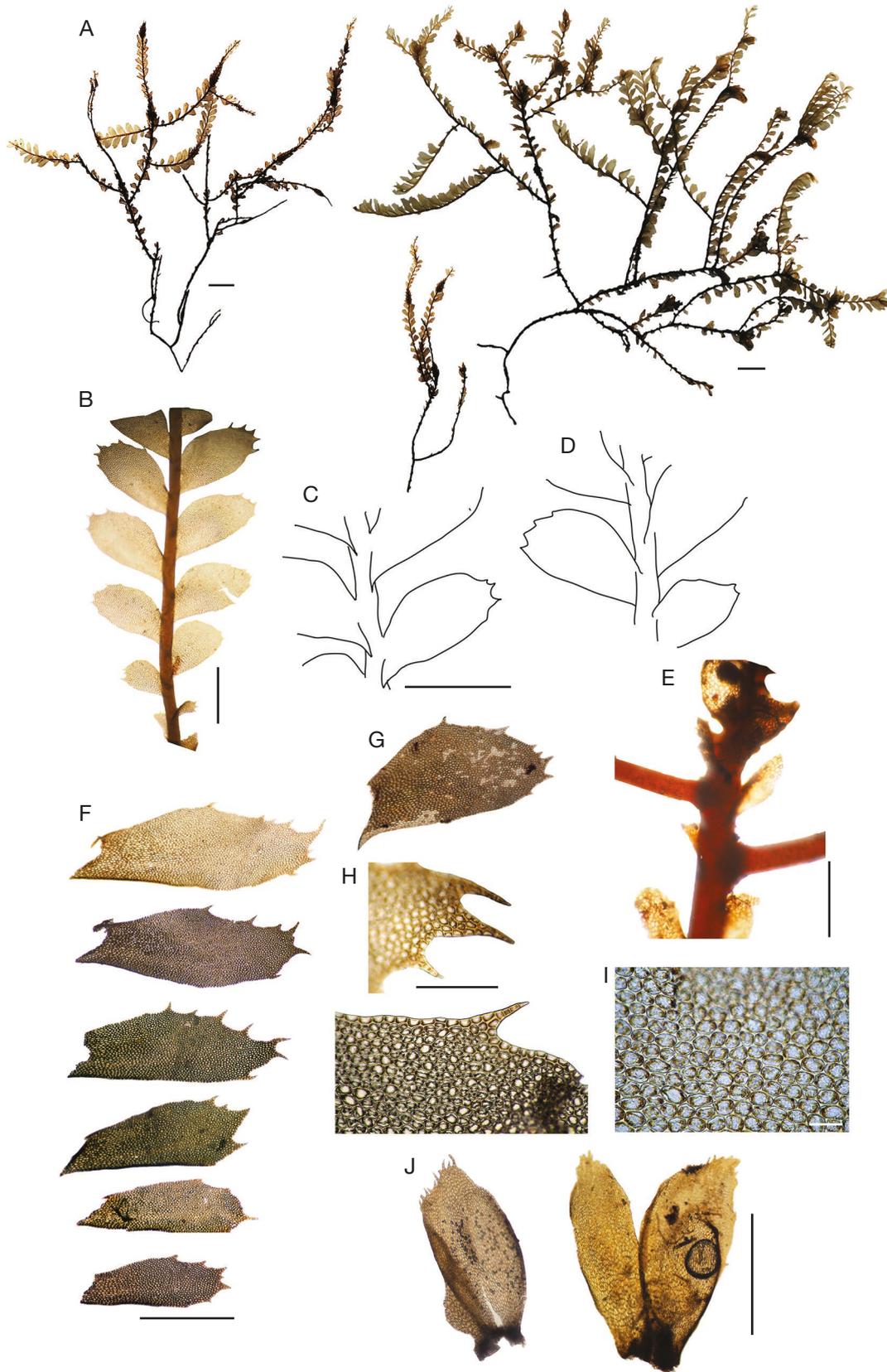


FIG. 12. — *Plagiobila pectinata* Lindenb.: **A**, habit; **B**, shoot in dorsal view; **C**, shoot in dorsal view; **D**, shoot in ventral view; **E**, intercalary branching; **F**, branch leaves; **G**, stem leaf; **H**, leaf margin showing teeth; **I**, midleaf cells; **J**, perianth. From *Tixier 9462, 9474* (PC). Scale bars: **A**, 5 mm; **B-D**, **F**, **G**, 1 mm; **E**, **I**, 0.5 mm; **J**, **H**, 0.25 mm.

*Plagiochila punctata* (Taylor) Taylor var. *punctata*  
(Vanden Berghen 1981: 56, fig. as *P. subalpina*)

*Jungermannia punctata* Taylor, *Transactions of the Botanical Society of Edinburgh* 1: 179 (1844). — *Plagiochila punctata* (Taylor) Taylor, *London Journal of Botany* 5: 261 (1846). — Type: **Ireland**. Unknown collector (FH?; *vide* Heinrichs *et al.* 2005b).

*Plagiochila subalpina* Steph., *Hedwigia* 30: 268 (1891), *nom. illeg.* — Type: **Tanzania** (Heinrichs *et al.* 2005b).

SPECIMENS EXAMINED. — **Madagascar**. Prov. Fianarantsoa • Ranomafana Nat. Park, E. ridge of Mt. Vohipanani, 1140-1230 m, VII.2003, *Pócs & Ranaivojaona 04121/CU* (EGR).

Additionally reported from Ambohimahasoa (*Onraedt 70M532*), c. 100 km N of the town of Fianarantsoa by Vanden Berghen (1981).

DISTRIBUTION AND HABITAT. — Afro-American: tropical America, Bioko, East Africa; also in western Europe. In Madagascar rare, found on bark, rock and soil in subhumid evergreen forests above 1000 m, in rather exposed environments.

DESCRIPTION (see also Vanden Berghen 1981; Fischer 2013, both as *P. subalpina*)

Plants very small, 0.5-1.5(-2) mm wide, *c.* 1-1.5 cm long, green to greenish-brown, becoming blackish-brown when dry, sparsely branched, branches intercalary, frequently denuded or flagelliform due to copious production of caducous leaves, rhizome-like shoot absent. Mature stem leaves distant to subimbricate, rather widely spreading, ventrad, obovate-suborbicular, 1-1.3× longer than wide, not ampliate, unbordered, apex rounded, margins plane, with 3-6 long, narrowly triangular teeth at the apex and on the upper half of the ventral margin, teeth made up of short cells, apex frequently bifid (to 1/3) or trifid by larger, lobe-like teeth; dorsal and ventral bases scarcely decurrent. Leaf cells subisodiametrical, *c.* 20-30 µm wide in midleaf, with small to large, swollen trigones, leaf base with a short vitta-like area of large cells; cuticle smooth; oil bodies not observed. Underleaves absent. Gametocidia not seen. Vegetative reproduction by caducous leaves, the caducous leaves similar to ordinary leaves or much smaller, deeply bifid.

NOTES

*Plagiochila punctata* (sect. *Arrectae*) is characterized by the small plants (0.5-1.5 mm wide) with numerous leafless shoots due to caducous leaves. The persistent leaves are rather widely spreading, ventrad, obovate-suborbicular, 1-1.3× longer than wide, with 3-6 rather long teeth at the apex and on the upper half of the ventral margin. The remnant leaves on denuded shoots are usually minute and deeply bifid.

*Plagiochila punctata* (Taylor) Taylor var. *paucidentata*  
(Mont. & Gottsche) Gradst., *comb. nov.*  
(Fig. 13)

*Plagiochila paucidentata* Mont. & Gottsche, *Annales des Sciences naturelles, Botanique* (sér. 4) 6: 197 (1856). — *Plagiochila mascarena* Gottsche, *Annales des Sciences naturelles, Botanique* (sér. 4) 8: 335

(1857), *nom. superfl.* — Type: **France**. La Réunion, *C. Richard s.n.* (lecto-, designated by Grolle [1995], PC0031004).

*Plagiochila emarginata* sensu Vanden Berghen (1981), non typus (*vide* Grolle 1995).

SPECIMENS EXAMINED. — **Madagascar**. Prov. Antsiranana • Marojejy Nat. Park, elfin forest on ridge, 1000-1400 m, III.1990, *Pócs et al. 90114/BG* (EGR as *P. pectinata*). — **Prov. Toamasina** • Andasibe-Mantadia Nat. Park, rocky ridge of Mt. Andrianavibe, 950-1050 m, X.1994, *Pócs & Szabo 9487/BQ*, det. J. Heinrichs as *P. punctata* (Heinrichs *et al.* 2005b) (EGR, GOET).

DISTRIBUTION AND HABITAT. — East African Islands (Madagascar, La Réunion; Mauritius?); first reported from Madagascar by Gottsche (1857 as *P. mascarena*; *vide* Grolle 1995), but this record was not mentioned in Vanden Berghen (1981). More recently, this variety has been found twice in Madagascar, growing on bark in ridge forest (elfin forest) at 950-1400 m. In La Réunion var. *paucidentata* occurs at slightly higher elevation, above 1500 m, on various substrates (bark, soil, rock) in exposed environments (Vanden Berghen 1981).

DESCRIPTION (see also Vanden Berghen 1981 as *P. emarginata*)

Plants 1-2 mm wide, 1-5 cm long, sparsely branched, branches intercalary, sometimes denuded by caducous leaves. Mature stem leaves distant to subimbricate, obliquely spreading, ventrad to subtransverse, obovate-oblong, 1.3-1.5(-2)× longer than wide, widest towards the apex, not ampliate, older stem leaves slightly bordered, apex broadly rounded, margins plane or slightly recurved, entire or with 1-5 small teeth near the apex, the teeth made up of short cells; leaf bases not or shortly decurrent. Leaf cells subisodiametrical, *c.* 20-30 µm wide in midleaf, trigones small to large and swollen, in older stem leaves becoming larger and confluent along the margin, forming a weakly defined border; leaf base with an ill-defined vitta-like area of larger cells; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia terminal, short, of 4-7 pairs of bracts. Perianth without stalk, perianth mouth with triangular teeth. Vegetative reproduction by caducous leaves, the caducous leaves similar to ordinary leaves.

NOTES

*Plagiochila punctata* var. *paucidentata* (Mont. & Gottsche) Gradst., *comb. nov.* differs from var. *punctata* in the more elongate, obovate-oblong leaves, 1.3-2× longer than wide, with margins entire or with 1-5 small teeth near apex. The trigones of leaf cells vary considerably in size and in older stem leaves the trigones tend to become larger and confluent along the margin, forming a weakly defined border.

*Plagiochila repanda* (Schwägr.) Lindenb. var. *repanda*  
(Fig. 14)

*Jungermannia repanda* Schwägr., *Historiae Muscorum Hepaticarum Prodrumus*: 26 (1814). — *Plagiochila repanda* (Schwägr.) Lindenb., *Species Hepathicarum* (fasc. 2-4): 62 (1840). — Type: **Mauritius**. Unknown collector (lecto-, designated by Grolle [1995], W; isolecto-, S).

*Plagiochila ligulata* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4 (4): 347 (1904). — Type: **Madagascar** (Grolle 1995).

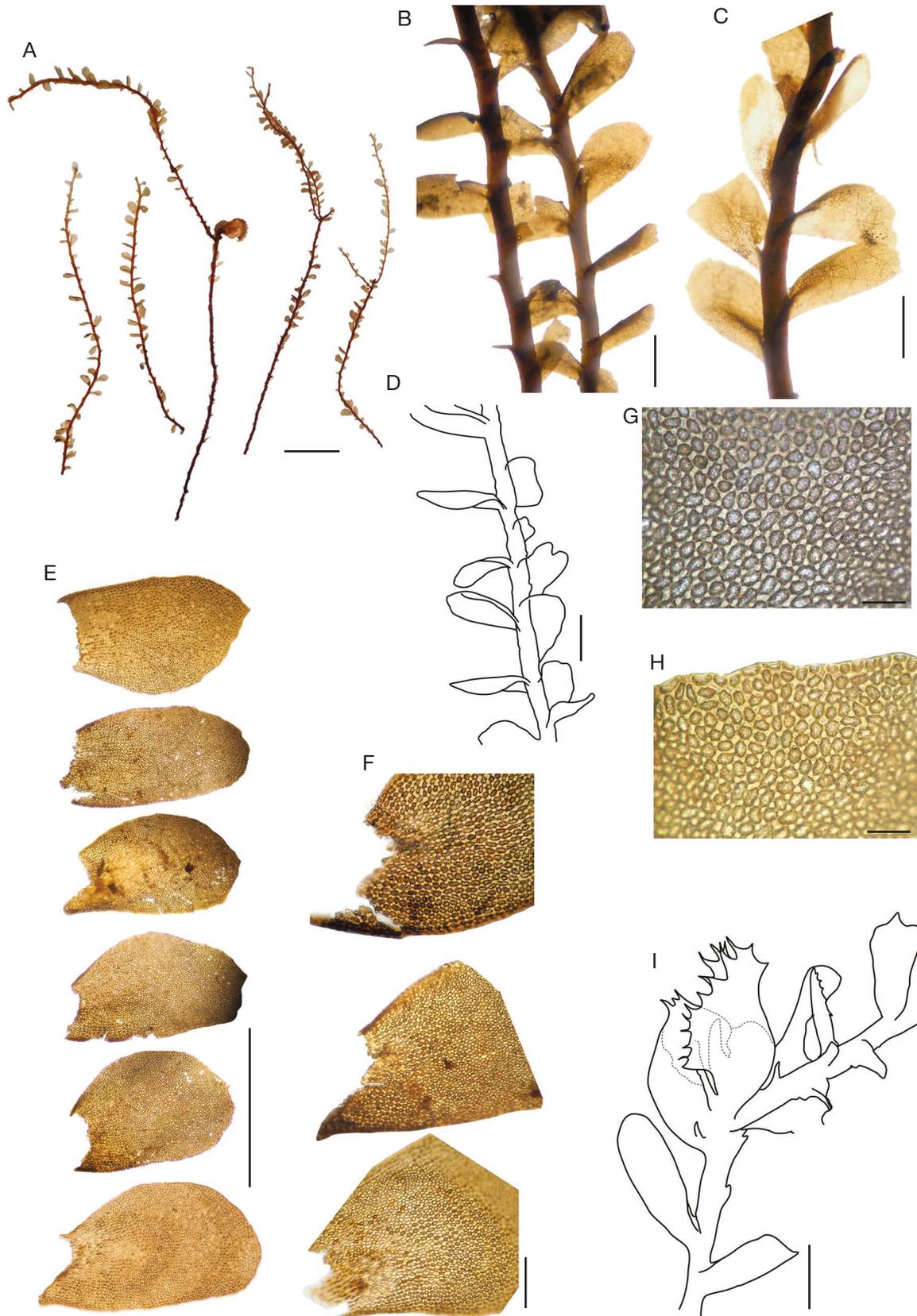


FIG. 13. — *Plagiobila punctata* (Taylor) Taylor var. *paucidentata* (Mont. & Gottsche) Gradst., comb. nov.: **A**, habit; **B**, shoots in ventro-lateral view; **C**, shoot in dorsal view; **D**, shoot in ventral view; **E**, leaves; **F**, leaf bases with vitta-like area; **G**, midleaf cells; **H**, leaf margin cells; **I**, female shoot with perianth and innovation. From Szabo 9640/CS, Pócs 0861/R (EGR). Scale bars: A, 5 mm; B-D, I, 0.5 mm; E, 1 mm; F, 0.1 mm; G, H, 0.05 mm.

*Plagiochila madagascariensis* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 344 (1882), *nom. inval.* (non Steph. 1904). — Type: **Madagascar** (Grolle 1995).

*Plagiochila nudiuscula* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 339 (1882). — Type: **Madagascar** (Grolle 1995).

*Plagiochila rutenbergiana* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 338 (1882), *nom. inval.* — Type: **Madagascar** (Stephani 1906; Grolle 1995).

**SPECIMENS EXAMINED.** — **Madagascar.** **Prov. Antananarivo** • Angavokely, I.1978, *Tixier 11112* (BR); Ankazobe, Ambohitantely Reserve, IX.1994, *Pócs 9444/AC* (EGR, GOET). — **Prov. Antsiranana** • Cuvette d'Andape, Mission catholique, VII.1971, *Onnaedt 70M5753* (PC). — **Prov. Fianarantsoa** • Analabé near Ambositra, VIII.1971, *Onnaedt 71M5817, 71.M5818* (BR); Nosiarivo, X.1976, *Tixier 9471*, det. Vanden Berghen as *P. barteri* (BR); Andringitra Nat. Park, tributary W of Korokoro river, IX.1994, *Pócs 9473/BA* (EGR); Ramomafana Nat. Park, beyond W park boundary, Mt. Namatoana, *Pócs & Tubá 04130/AQ* (EGR). — **Prov. Toamasina** • Masoala Peninsula W coast, slopes E of Ambanizana village, *Pócs 9448/B* (EGR); Andasibe (Perinet), III.1974, *Cremers 3142* (BR); VIII.1977, *Tixier 10672* (BR); Andasibe-Mantadia Nat. Park, III.1990, *Pócs et al. 90103/A, 90103/AE, 90103/G, 90103/L* (EGR), *90106/N* (EGR, GOET); X.1994, *Pócs 9485/P* (EGR).

**DISTRIBUTION AND HABITAT.** — East Africa (Kenya, Tanzania, Malawi) and East African Islands (Madagascar, La Réunion, Mauritius). In Madagascar growing on bark in humid to subhumid evergreen forests, also on tree ferns, 400-1500 m.

**DESCRIPTION** (see also Jones 1962; Vanden Berghen 1981) Plants 2-4.5 mm wide, to 10 cm long, slightly and irregularly pinnately branched or unbranched, branches mostly intercalary, occasionally terminal, dorsal stem surface without paraphyllia. Creeping, rhizome-like primary stem present. Mature stem leaves imbricate, obliquely to widely and ± horizontally spreading, ovate-rectangular to ovate-triangular, *c.* 1.5-2.5× longer than wide, usually ampliate, the expanded ventral leaf bases sometimes forming a crest, apex rounded to truncate, entire or with 1-8 small teeth (teeth 1-4 cells long), not bifid, ventral margin usually entire, occasionally with a few irregular teeth, dorsal margin entire; dorsal leaf bases entire, rather shortly and broadly decurrent, inflated, almost concealing the stem, ventral bases shortly to moderately and narrowly decurrent, the linear decurrent portion to 0.2 mm long. Leaf cells subsisodiametrical, 15-25 µm wide in midleaf, with small to large, swollen trigones, cells smaller and subquadrate to rectangular along the margin and usually with larger, sometimes confluent trigones, forming a weak border in robust plants; vitta-like area at the base present or absent, cells in the dorsal leaf base not elongate; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia terminal to intercalary, with 3-6 pairs of bracts. Perianth campanulate, base without stalk, mouth with numerous narrowly triangular teeth or cilia. Vegetative reproduction by leaf fragmentation.

#### NOTES

*Plagiochila repanda* var. *repanda* (sect. *Vagae*) is recognized by the wide-spreading, ovate-rectangular leaves with an ampliate ventral base and leaf margins ± entire or with a few small teeth

(up to 8) at apex. The leafy stems arising from the creeping rhizome-like shoot are long and sparsely branched by intercalary branching (very rarely terminal). Very characteristic are the rather small, subsisodiametric leaf cells, 15-25 µm wide in midleaf, with frequently large bulging trigones (but sometimes trigones small). When the trigones are large, the leaf is rather opaque. The trigones tend to become larger and confluent at the leaf margin, and the thicker-walled margin cells may form an ill-defined border. The cells at the leaf base are sometimes enlarged, forming a vitta-like area (e.g. in *Tixier 9471*, det. Vanden Berghen as *P. barteri*).

*Plagiochila repanda* var. *perrotana* (Steph.) Vanden Bergh. (Fig. 15)

*Plagiochila perrotana* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 4 (6): 586 (1904). — Type: **Madagascar.** Tamatave, 1896, *Bryotheca Levier 347* (lecto-, designated here [Vanden Berghen 1981 as "holotype"], G00065763!); 1897, in silva "Fito", *Perrot s.n.*, *Bryotheca Levier 1214* (syn-, G00068921!).

*Plagiochila liliputana* sensu Vanden Berghen (1981), non typus (see below).

**SPECIMENS EXAMINED.** — **Madagascar.** **Prov. Mahajanga** • Seuil de Mandritsara, Jardin Botanique, *c.* 850 m, *Morat 4532a* (BR). — **Prov. Toliara** • Tôlanaro ("Fort Dauphin"), on trees in primary forest, *c.* 20 m, VI.1971, *Onnaedt 70M5561* (BR 2 specimens as *P. liliputana*, det. Vanden Berghen). — **Prov. Toamasina** • Andasibe-Mantadia Nat. Park, III.1990, *Pócs et al. 90106/H, 90106/J, 90108/X* (EGR); Saharanga river valley, X.1994, *Pócs 9484/P* (EGR); Anosibe, IV.1978, *Tixier 11745* (BR); Analabé, XII.1975, *Tixier 7872* (BR).

**DISTRIBUTION AND HABITAT.** — East African Islands (Comores, Madagascar, La Réunion, Mauritius). In Madagascar on bark and rotten wood in humid to subhumid mid-elevation forests and plantations, 850-1050 m; exceptionally at sea level.

#### NOTES

*Plagiochila repanda* var. *perrotana* is identical to var. *repanda* except for the mostly bifid leaf apex; in var. *repanda* the apex is entire or toothed, not bifid. The two teeth at the leaf apex in var. *perrotana* vary considerably in size and in the specimen from Madritsara (*Morat 4532a*) they are very long, up to ten cells long.

A collection from lowland elevation ("Fort Dauphin", *Onnaedt 70M5561*) identified by Vanden Berghen (1981) as *P. liliputana*, stands out by small plant size (1.5-2 mm wide) and rather distant leaves with ventral bases not or scarcely ampliate. In other respects, the plants are identical to *P. repanda* var. *perrotana*. We interpret the specimen as a weak lowland phenotype.

*Plagiochila rodriguezii* Steph. (Fig. 16)

*Plagiochila rodriguezii* Steph., *Botanical Gazette* 15: 290 (1890). — Type: **France.** La Réunion, 1889, *Rodriguez 140* (lecto-, designated here, G00045515!; isolecto-, PC0102937!, PC0102938!).

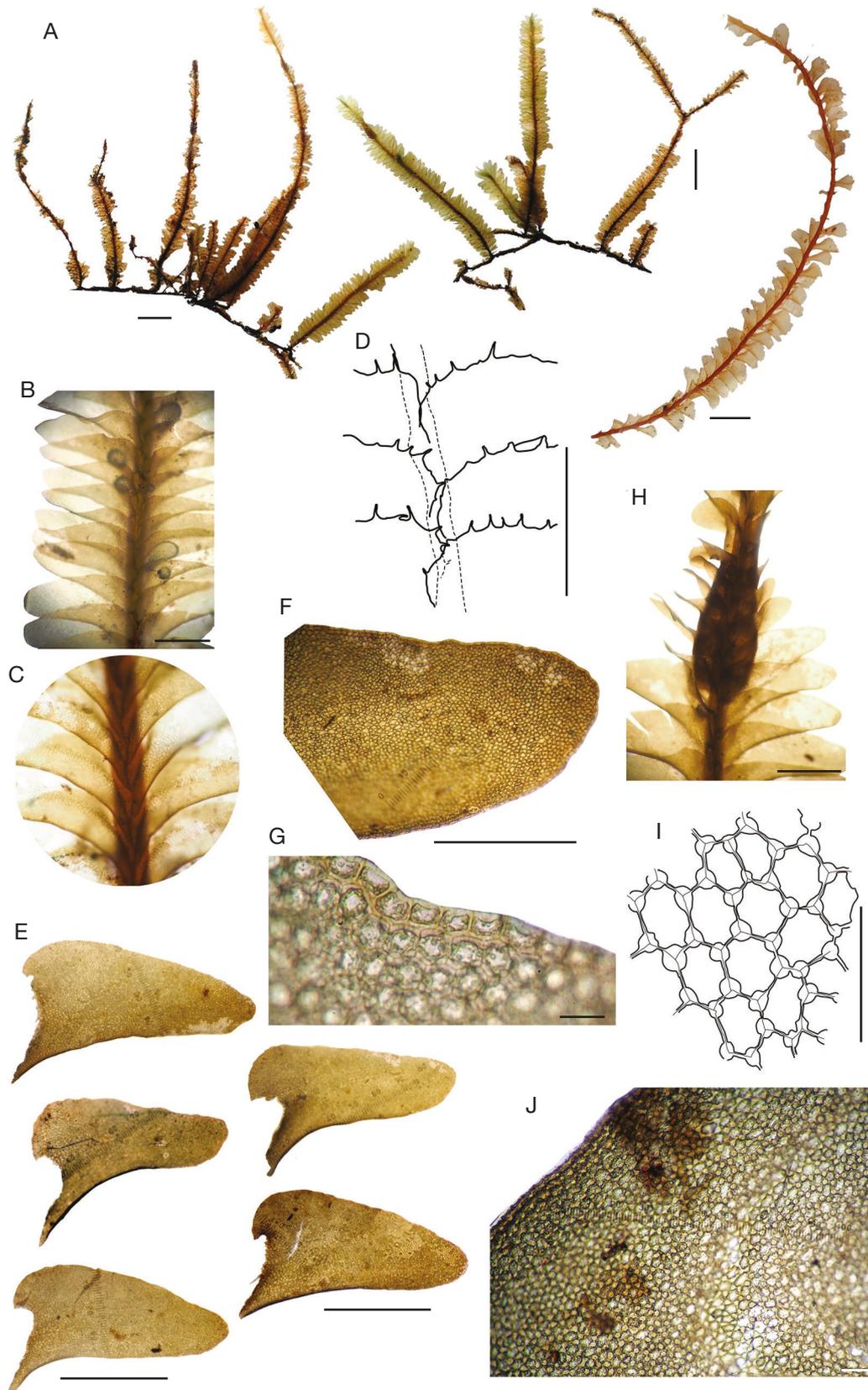


FIG. 14. — *Plagiobola repanda* (Schwägr.) Lindenb. var. *repanda*: **A**, habit; **B**, **C**, shoots in dorsal view; **D**, shoot in ventral view, showing ampliate leaf bases; **E**, leaves; **F**, leaf apex; **G**, leaf margin bordered by subquadrate to rectangular cells; **H**, shoot with terminal androecia; **I**, **J**, midleaf cells. From Pócs 90103/AE (EGR). Scale bars: **A**, 5 mm; **B**-**E**, 1 mm; **F**, 0.5 mm; **G**-**J**, 0.05 mm.



FIG. 15. — *Plagiochila repanda* var. *perrotana* (Steph.) Vanden Bergh. : **A**, leaves; **B**, portion of leaf. From Pócs 90106H (EGR). Scale bars: A, 1 mm; B, 0.5 mm.

*Plagiochila liliputana* Herzog, *Botaniska Notiser* 101: 232 (1947). — Type: Comores (Grolle 1995).

ADDITIONAL SPECIMENS EXAMINED. — **Madagascar**. Prov. **Antsiranana** • Marojejy Nat. Park, III.1990, Pócs et al. 90115/F (EGR). — Prov. **Fianarantsoa** • near Ambositra, I.1970, Onraedt 70M41, 70M361 (BR); Andringitra Nat. Park, tributary W of Korokoro river, IX.1994, Pócs 9473/AV (EGR). — Prov. **Toamasina** • near Moramanga, I.1970, Onraedt 70M2034 (BR).

DISTRIBUTION AND HABITAT. — East Africa (Tanzania), East African Islands (Comores, Madagascar, La Réunion). In Madagascar found on bark in humid evergreen forests at 1000–1800 m.

DESCRIPTION (see also Vanden Berghen 1981)

Plants 2.5–3 mm wide, to 5 cm long, rather rigid, irregularly pinnate, becoming dichotomous in younger parts, branches mostly terminal, few intercalary branches. Creeping, rhizome-like shoot present, long. Stem surface without paraphyllia. Mature stem leaves imbricate and ventrad, obliquely spreading, asymmetrically ovate-triangular, *c.* 1.5× longer than wide, ± ampliate, margins unbordered, ventral margin arched and deeply undulate-crispate from base to near apex, undulations entire or with 1–several sharp, to 10 cells long triangular teeth, the teeth up to 20 per leaf, dorsal margin almost straight, narrowly recurved and entire or with 1–2 short teeth; dorsal bases longly broadly decurrent, partly to entirely covering the stem, ventral bases shortly and very narrowly decurrent, the decurrent part entire. Leaf cells subrectangular, 10–20 µm wide in midleaf, trigones small to large and confluent, cell-lumina rounded to flexuose-angular; leaf base with a short vitta-like area; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia terminal to intercalary, of 4–10 pairs of bracts. Perianth without stalk, perianth mouth densely toothed by shortly triangular teeth. Vegetative reproduction not observed.

#### NOTES

*Plagiochila rodriguezii* (sect. *Vagae*) is readily recognized by the rigid, irregularly (bi)pinnate to dichotomous plants with terminal and intercalary branches, ventrad leaves with strongly undulate-crispate ventral margins without or with several (to 15) long and sharp teeth, small leaf cells (10–20 µm wide in midleaf), and absence of underleaves. In the type material the undulate ventral leaf margins are subentire but in the collections made by Pócs (EGR) they are strongly toothed.

In the branching type and undulate-crispate ventral margins, *P. rodriguezii* is similar to *P. squamulosa* and *P. corrugata* but the ventral leaf bases in the latter two species are broadly and longly decurrent and ciliate-laciniate, underleaves are present and the leaf cells are slightly larger. Moreover, *P. squamulosa* has paraphyllia.

*Plagiochila rodriguezii* shares undulate ventral leaf margins and shortly decurrent leaf bases with *P. africana* Steph. from West Africa. The latter species clearly differs from *P. rodriguezii*, however, in purely dichotomous branching, leaves horizontally spreading and very flat, ventral leaf base not ampliate but with a low shoulder (which may be differentiated into a small, inflated auricle on older leaves), larger leaf cells, *c.* 25 µm wide in midleaf, and presence of distinct underleaves (see Jones 1962). *Plagiochila africana* is close to *P. boivinii* (see under the latter species).

*Plagiochila liliputana* Herzog, described from the Comores and a synonym of *P. rodriguezii* according to Grolle (1995), was reported from Madagascar by Vanden Berghen (1981). The Madagassan plant is a very different plant and a synonym of *P. repanda* var. *perrotana*.

#### *Plagiochila sikorae* Steph.

(Fig. 17)

*Plagiochila sikorae* Steph., *Bulletin de la Société royale de Botanique de Belgique* 32 (2): 37 (1893). — Type: Madagascar. Without locality, 1891, *Sikora* 85 p.p., *c. andr.* (holo-, G00045519).

ADDITIONAL SPECIMENS EXAMINED. — **Madagascar**. Prov. **Antsiranana** • Manongarivo-Ambahatra Reserve, ridge between the two branches of Ambahatra Mt., 850–950 m, III.1999, *Geissler 19459* (EGR, G, GOET); Marojejy Nat. Park, elfin forest on ridge, 1000–1400 m, III.1990, Pócs et al. 90114/DC (EGR as *P. repanda*). — Prov. **Fianarantsoa** • Andringitra Nat. Park, Ambavafatra, heath forest at the N foot of Mt. Vohipia, 1270–1350 m, IX.1994, Pócs 9477/D, *c.gyn.* (EGR); Ranomafana Nat. Park, E. ridge of Mt. Vohipanani, 1140–1230 m, VII.2003, Pócs & Ranaivojoana 04121/CS (EGR); Namorona river, 1080–1150 m, VII.2003, Pócs & Ranaivojoana 04126/AT (EGR, GOET). — Prov. **Toamasina** • pont Sanjouin between Moramanga and Anosibe, 900 m, I.1970, Onraedt 70M0354 (BR); Andasibe-Mantadia Nat. Park, rocky ridge of Mt. Andrianavibe, 950–1050 m, X.1994, Pócs 9487/BQ (EGR, GOET).

DISTRIBUTION AND HABITAT. — Only known from Madagascar, where it grows on moist rock, rotten wood and bark in primary subhumid mid-elevation forest and heath forest, 850–1400 m.

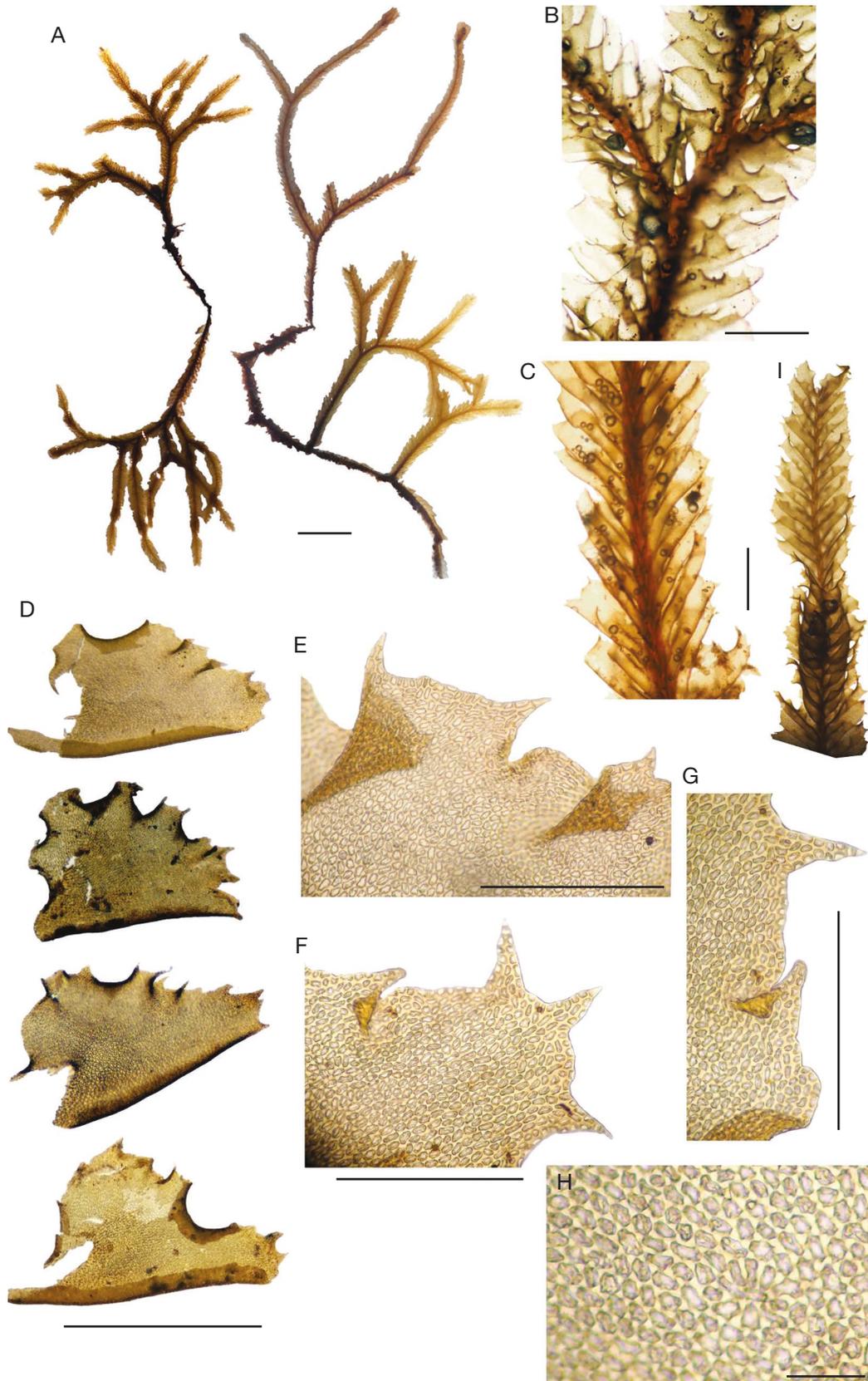


FIG. 16. — *Plagiobila rodriguezii* Steph.: **A**, habit; **B**, shoot in ventral view with terminal branch; **C**, shoot in dorsal view; **D**, leaves; **E**, **G**, portion of leaf margin; **F**, leaf apex; **H**, midleaf cells; **I**, branch with intercalary androecia. From Pócs 90115/F (EGR). Scale bars: A, 5 mm; B-D, 1 mm; E-G, 0.25 mm; H, 0.05 mm; I, 1 mm.

DESCRIPTION

Plants *c.* 1.5-2 mm wide and to 4 cm long, unbranched or sparsely branched, branches intercalary, normal-leaved or flagelliform. Creeping rhizome-like stem present. Dorsal surface of stem with scattered paraphyllia along the dorsal midline, between the dorsal leaf bases. Stem leaves imbricate, falcato-secund when dry, obliquely to widely spreading when moist, ampliate, ovate to narrowly ovate-triangular, 1-2× longer than wide, often fragmenting, margins entire to toothed by few shortly linear to narrowly triangular teeth (1-3 cells long) made up of rather short cells, apex with 0-5 short teeth, ventral margin with 0-10 teeth, dorsal margin entire or with 1-7 teeth at the base (like in *P. barteri*); dorsal bases shortly to moderately decurrent, strongly swollen, mostly covering the stem, ventral bases shortly and narrowly decurrent. Leaf cells irregularly subisodiametrical, 20-30 µm wide in midleaf, with triangular to trabeculate trigones, leaf base with a very short (rudimentary) vitta-like area of larger cells, cells in the dorsal leaf base not elongate; cuticle smooth; oil bodies not observed. Underleaves absent. Gynoecia usually with two innovations, bracts larger than leaves, upright, strongly fragmenting, broadly ovate-triangular, *c.* 2.5-3 × 1.5-2 mm, toothed all along the margin, with numerous short teeth. Perianth ovate-oblong in outline, *c.* 2 mm long, not extending beyond the bracts, swollen, the mouth with numerous short, *c.* 2-3 cells long cilia and lacinia, perianth base not stalked. Vegetative reproduction by leaf fragmentation.

NOTES

*Plagiochila sikorae* (sect. *Africanae*) is a delicate, 1-2 mm wide species with long, sparsely branched stems (branching purely intercalary) and with small paraphyllia on the dorsal stem surface, between the leaf bases. The leaves are ovate to ovate-triangular, ± fragmenting and falcato-secund to widely spreading, with ampliate ventral bases and margins with few small teeth, 1-5 at the apex, 0-10 on the ventral margin and 0-7 on the dorsal base; the dorsal leaf bases are conspicuously decurrent, strongly swollen, usually toothed and are covering much of the stem surface, while the ventral bases are shortly decurrent. The leaf cells are almost isodiametrical, with triangular to trabeculate trigones, and are not elongate towards the base. The species is close to *P. barteri* and was treated as a synonym of the latter species by Vanden Berghen (1981); both species share toothed dorsal leaf bases. However, *P. barteri* lacks dorsal stem paraphyllia and is a more robust plant (to 5 mm wide), the leaves are more strongly toothed, with 20-50 teeth, and not falcato-secund when dry.

*Plagiochila simplex* (Sw.) Lindenb.  
(Fig. 18)

*Jungermannia simplex* Sw., *Nova Genera et Species Plantarum seu Prodromus*: 145 (1788). — *Plagiochila simplex* (Sw.) Lindenb., *Species Hepathicarum* (fasc. 2-4): 54 (1840). — Type: **Jamaica**. *Swartz s.n.* (holo-, S!).

ADDITIONAL SPECIMENS EXAMINED. — **Madagascar**. Prov. Fianarantsoa • Andringitra Nat. Park, ridge 6 km E of Pic Boby, IX.1994, *Pócs 9475/H* (EGR, GOET).

DISTRIBUTION AND HABITAT. — Afro-American: tropical America (widespread), Madagascar (new); new to Africa. In Madagascar found on bark in elfin forest dominated by bamboos at 1450-1700 m.

DESCRIPTION (see also Heinrichs *et al.* 1998)

Plants small, 1.5-2 mm wide, to 4 cm long, irregularly pinnate, branches intercalary. Creeping, rhizome-like primary stem present. Mature stem leaves distant to contiguous, obliquely to widely spreading, strongly ventrad, asymmetrically ovate to oblong, 1.3-2× longer than wide, widest in the middle, often caducous, base not ampliate and not shouldered, apex irregularly rounded to truncate, often bifid, margins unbordered, curved, toothed near apex by 2-12 short, triangular teeth, the teeth 1-3(-4) cells long, the apex sometimes with two larger, lobe-like teeth, the teeth on the ventral margin extending downwards to the lower 1/3 and becoming progressively smaller below, dorsal margin and leaf bases entire; leaf bases shortly and narrowly decurrent, decurrent ventral part *c.* 0.1 mm long. Leaf cells subisodiametrical, *c.* 20-35 µm wide in midleaf, 1-1.5× longer than wide, with rather small radiate trigones, cells not thicker-walled to the margin, leaf base without vitta-like area; cuticle smooth; oil bodies not observed. Underleaves absent. Androecia not seen. Perianths on a short stalk, base not covered by bracts. Vegetative reproduction by caducous leaves.

NOTES

*Plagiochila simplex* (sect. *Heteromallae*) is a widespread neotropical specides that was recored from La Réunion by Lindenberg (1840). The record from La Réunion has not been confirmed, however, and the species was excluded from Africa by Grolle (1995) and Wigginton (2018). The occurrence of *P. simplex* in Africa is here confirmed. Characteristic are the flaccid plants with obliquely spreading, ventrad, frequently caducous ovate-oblong leaves that are less than 2× longer than wide, with small teeth at apex and along the ventral margin, subisodiametric leaf cells with small radiate trigones, no vitta, and perianths on a short stalk. The species is close to *P. pectinata* but the leaves in the latter species are more elongate (2-3× longer than wide), leaf cells rectangular and perianths not stalked.

*Plagiochila squamulosa* Mitt.  
(Fig. 19)

*Plagiochila squamulosa* Mitt., *Journal of the Proceedings of the Linnean Society, Botany* 7: 165 (1864). — Type: **Cameroun**. Mt. Cameroun, *Mann s.n.* (holo-, BM; iso-, NY; *vide* Grolle 1995).

*Plagiochila crispulocaudata* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 340 (1882). — *Plagiochila squamulosa* var. *crispulocaudata* (Gottsche) Vanden Bergh., *Bulletin du Jardin botanique national de Belgique* 51: 74 (1981). — Type: **Madagascar** (Vanden Berghen 1981).

*Plagiochila sinuosa* Mitt., *Journal and Proceedings of the Linnean Society of London* 22: 319 (1886). — *Plagiochila squamulosa* var. *sinuosa* (Gottsche) Vanden Bergh., *Bulletin du Jardin botanique national de Belgique* 51: 74 (1981). — Type: **Tanzania** (Vanden Berghen 1981). Reported from Madagascar by Stephani (1906).

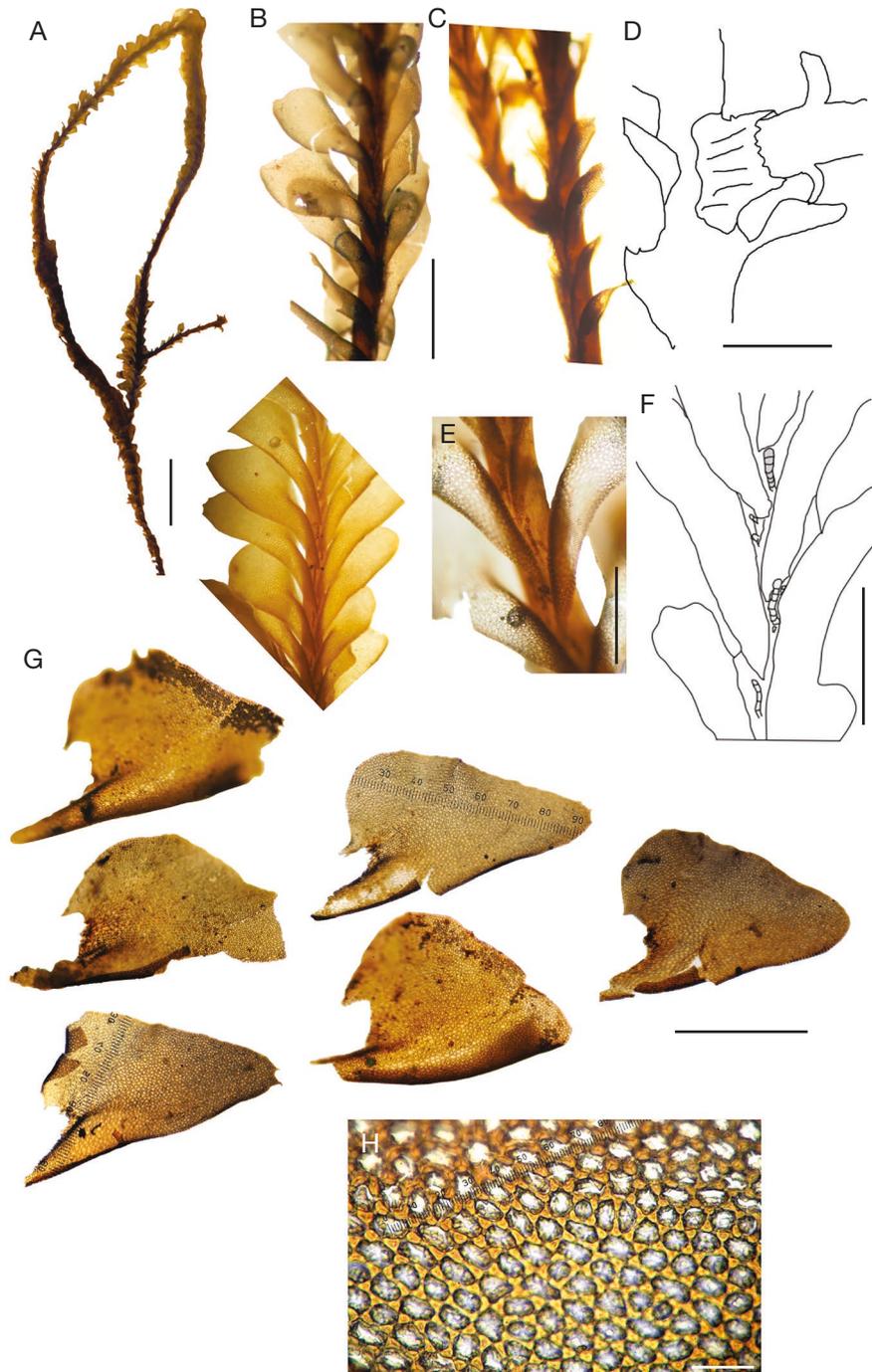


FIG. 17. — *Plagiochila sikorae* Steph.: **A**, habit; **B**, habit in dorso-lateral view, showing ventrad habit of leaves; **C**, habit in dorso-lateral view, showing intercalary branching; **D**, intercalary branching; **E**, **F**, stem in dorsal view showing paraphyllia; **G**, leaves; **H**, midleaf cells. From Pócs 9477/D (EGR). Scale bars: A, 5 mm; B, C, G, 1 mm; D-F, 0.5 mm; H, 0.05 mm.

**SPECIMENS EXAMINED.** — Madagascar. **Prov. Antananarivo** • Manjakatampo Reserve, Tavolotara Forest, 2100 m, XII.2017, Reeb 17M503 (PC); Vakinankaratra, 1733 m, XII.2017, Reeb 7M401 (PC). — **Prov. Fianarantsoa** • Andringitra Nat. Park, near Antanifotsy, trail to Pic Boby, IX.1994, Orbán 9463/AI (EGR).

**DISTRIBUTION AND HABITAT.** — Bioko, East Africa, Madagascar, La Réunion; recorded from Madagascar by Vanden Berghen (1981) without citation of material. In Madagascar found on rock in secondary grassland with ericaceous bushes, 1900-2000 m.

**DESCRIPTION** (see also Jones 1962 as *P. crispulocaudata* and *P. squamulosa*; Vanden Berghen 1981) Plants 3-3.5 mm wide, to 4 cm long, rather rigid, irregularly pinnate, branches terminal and intercalary. Creeping, rhizome-like primary stem present. Ventral stem surface with small paraphyllia between the decurrent strips of the ventral leaf margin, the paraphyllia consisting of short rows of rounded cells. Mature stem leaves densely imbricate and ventrad, obliquely spreading, very asymmetrical, ovate-triangular, *c.* 1-1.5× longer than wide, strongly ampliate, margin

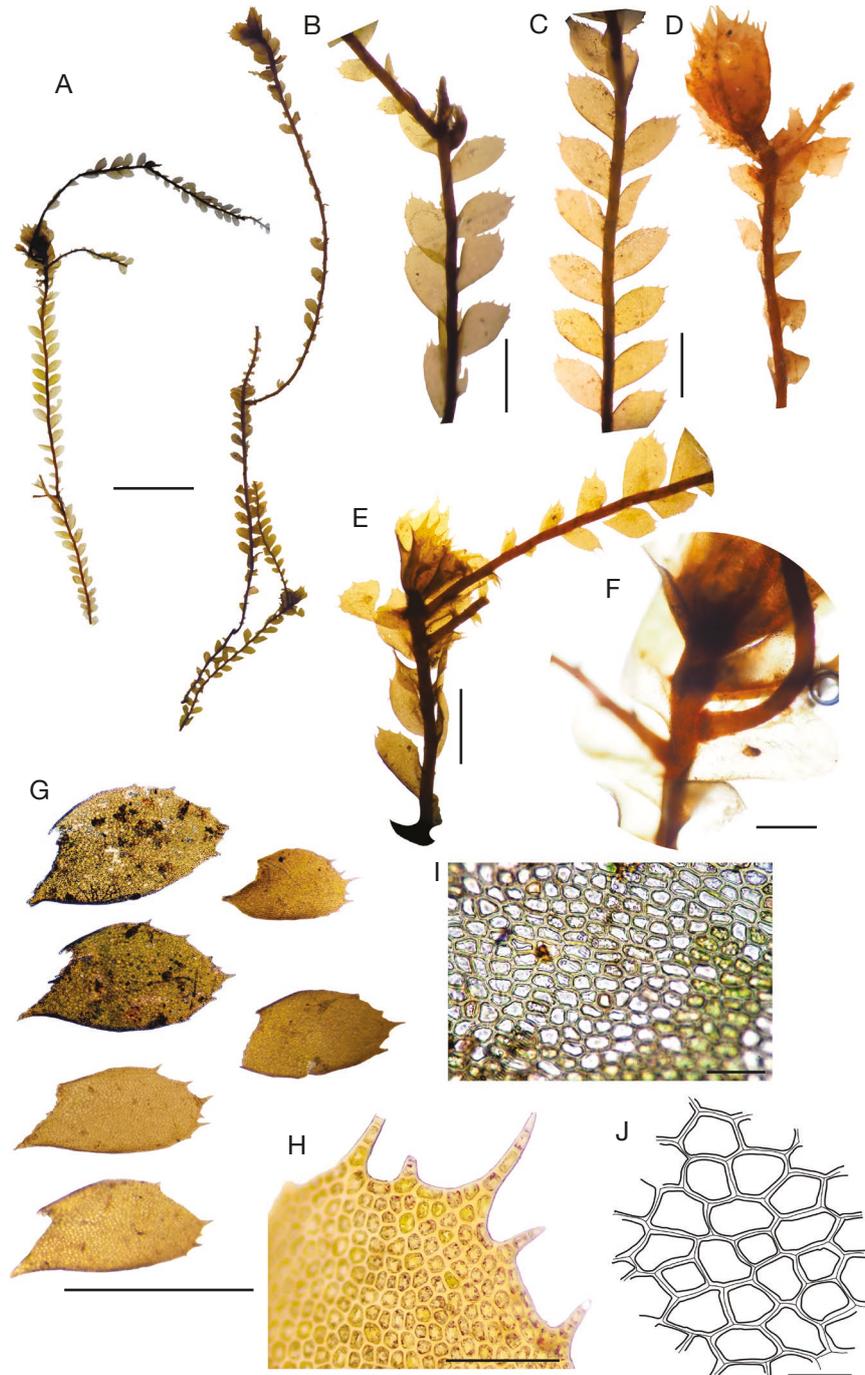


FIG. 18. — *Plagiochila simplex* (Sw.) Lindenb.: **A**, habit; **B**, shoot in dorsal view, with intercalary branch; **C**, shoot in dorsal view; **D-F**, shoot in ventral view with intercalary branching and stalked perianth; **G**, leaves; **H**, leaf apex; **I**, **J**, midleaf cells. From Ecuador, *Gradstein 12633* (GOET, QCA). Scale bars: A, 5 mm; B-E, G, 1 mm; F, 0.5 mm; H, 0.01 mm; I, 0.05 mm; J, 0.025 mm.

unbordered, apex broadly rounded, ventral margin undulate in the lower half, margins subentire or with up to 8 short, 1-2 cells long teeth on the apical margin; dorsal bases longly and very broadly decurrent, entirely concealing the stem, ventral base shortly to rather longly decurrent, the decurrent slightly undulate. Leaf cells subisodiametrical, *c.* 18-25  $\mu$ m wide in midleaf, with cordate to symmetrically swollen trigones; vitta-like area absent; cuticle smooth; oil bodies not observed. Underleaves

small to large, ciliate-laciniate. Androecia terminal to intercalary, of 4-10 pairs of bracts. Perianth without stalk, perianth mouth densely toothed by shortly triangular teeth. Vegetative reproduction not observed.

NOTES

*Plagiochila squamulosa* (sect. *Vagae*) is a common and variable species in the mountains of East Africa; several varieties

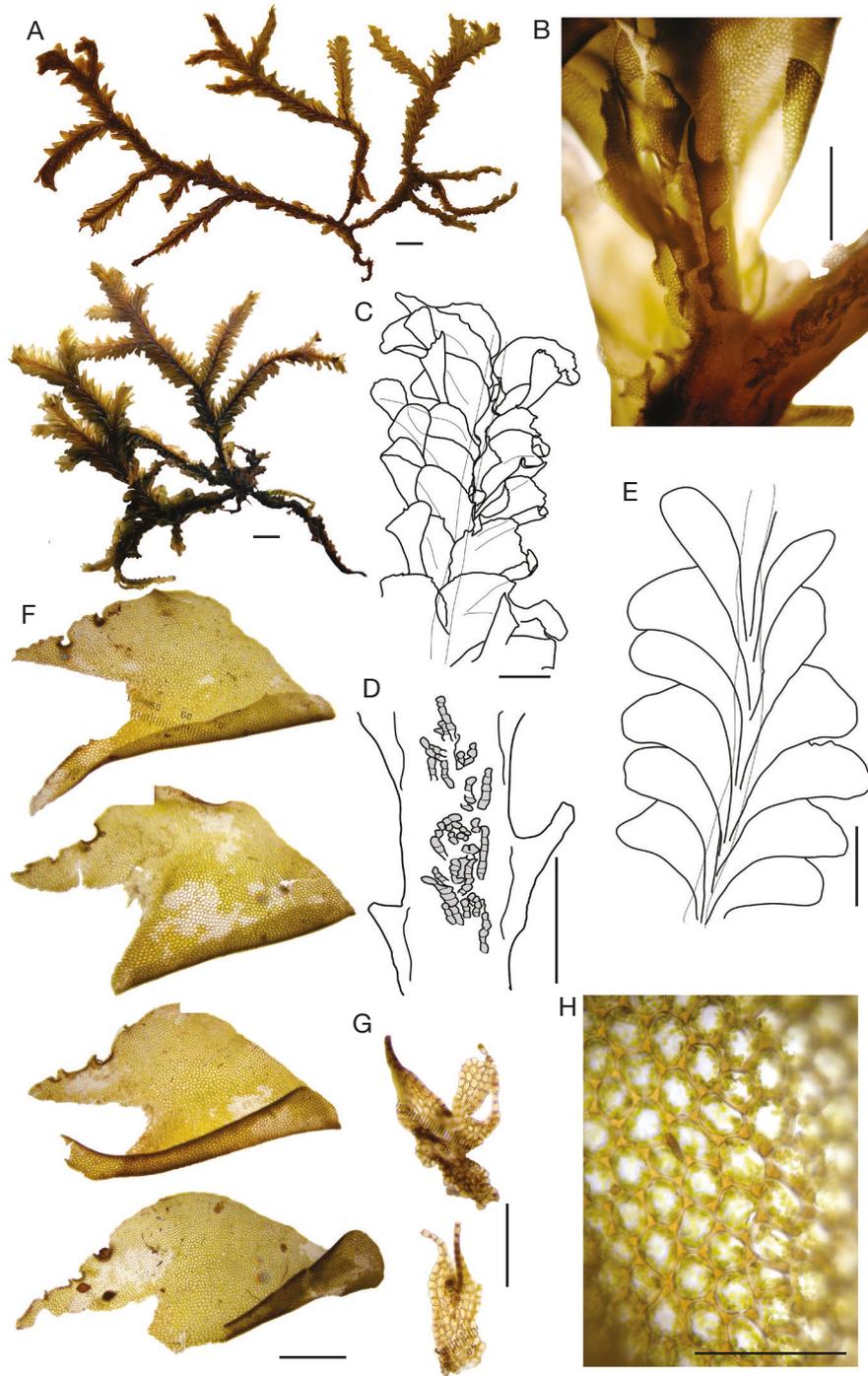


FIG. 19. — *Plagiochila squamulosa* Mitt.: **A**, habit; **B**, **C**, shoot in ventral view; **D**, shoot in ventral view with some leaves removed, showing paraphyllia; **E**, shoot in dorsal view; **F**, leaves; **G**, underleaves; **H**, midleaf cells. From Reeb CR17M503 (PC, TAN). Scale bars: A, 5 mm; B-D, G, 0.25 mm; E, F, 1 mm; H, 0.05 mm.

have been described (Jones 1962; Vanden Berghen 1981). The species is close to *P. corrugata* but differs from the latter in the presence of small paraphyllia on the ventral stem surface (consisting of short rows of rounded cells) and the ventral leaf margin being undulate only in the lower half and usually toothed. The examined Madagassan material of *P. squamulosa*, however, stands out by leaf margins with very few teeth.

*Plagiochila stricta* Lindenb.  
(Fig. 20)

*Plagiochila stricta* Lindenb., *Species Hepathicarum* (fasc. 1): 20 (1839). —Type: **Jamaica**. Swartz *s.n.* (holo-, W!).

ADDITIONAL SPECIMENS EXAMINED. — **Madagascar**. Prov. **Antananarivo** • between Ambatolaona and Mandraka, Pócs *et al.* 9868/

*AF* (GOET). — **Prov. Antsiranana** • Marojejy Nat. Park, III.1990, *Pócs 90114/CG* (EGR).

DISTRIBUTION AND HABITAT. — Peri-Afro-American (tropical America, Madagascar, Comores), also in Macaronesia (Lindner *et al.* 2004). In Madagascar found on bark in humid mid-elevation forest, 1000-1400 m.

DESCRIPTION (see also Heinrichs *et al.* 1998; Lindner *et al.* 2004)

Plants 2-3.5 mm wide, to 4 cm long, sparsely branched, branches intercalary. Creeping, rhizome-like primary stem present. Mature stem leaves usually imbricate, ± widely spreading, not ventrad, asymmetrically ovate-oblong, *c.* 1.5× longer than wide, widest at the base, not or slightly ampliate, unbordered, apex rounded, dorsal margin entire, ventral and apical margin with 5-20 narrowly triangular to linear teeth, the teeth to 4 cells long; dorsal and ventral bases shortly decurrent. Leaf cells isodiametrical to somewhat elongate, 15-30(-35) µm wide in midleaf, with conspicuous trigones, leaf base with a short vitta-like area; cuticle slightly to strongly striate-papillose; oil bodies not seen. Underleaves absent. Perianth base covered by leaves. Vegetative reproduction not observed (by caducous teeth?).

#### NOTES

*Plagiochila stricta* (sect. *Arrectae*) is recognized by the medium-sized plants (*c.* 2-3 mm wide) with rather wide-spreading, asymmetrically ovate-oblong leaves with up to 20 narrowly triangular to linear teeth, a short vitta and a finely papillose cuticle. The papillosity of the cuticle varies and the plants from Marojejy Reserve are only slightly papillose. *Plagiochila stricta* shares a papillose cuticle with *P. boryana* but the latter species is a much more robust plant with much larger leaf cells.

#### *Plagiochila strictifolia* Steph. (Fig. 21)

*Plagiochila strictifolia* Steph., *Hedwigia* 30: 210 (1891). — Type: **Cameroun**. Etome, *c.* 250 m, *Dusén 4* (holo-, G; iso-, BM; *vide* Jones 1962).

SPECIMEN EXAMINED. — **Madagascar**. **Prov. Toamasina** • W coast of Masoala Peninsula, S of Ambanizana village, IX.1994, *Pócs et al. 9446/P* (EGR).

DISTRIBUTION AND HABITAT. — Tropical African lowland species, widely distributed in West Africa, rarer in East Africa (Wigginton 2004); new to Madagascar. In Madagascar found on bark in remnant humid lowland forest at sea level.

DESCRIPTION (see also Jones 1962; Wigginton 2004)

Plants 2-2.5 mm wide, to 5 cm long, flaccid, dichotomous, branches mostly terminal, intercalary branches very few. Creeping, rhizome-like primary stem present. Leaves contiguous, obliquely diverging from the stem in the basal half (at *c.* 50°) and conspicuously arching outwards, horizontally spreading (not ventrad), symmetrically oblong-rectangular, *c.* 2-2.5× longer than wide, not or very slightly ampliate,

apex rounded to subtruncate, plane or slightly undulate, dorsal margin concave, ventral margin convex, the two margins conspicuously running parallel, entire or with 1-4 small triangular teeth at the apex and along the upper ventral margin; dorsal leaf base shortly decurrent, ventral leaf base very shortly decurrent, decurrent part to 0.1 mm long. Leaf cells small, isodiametrical to slightly elongate, *c.* 15-20 µm wide in midleaf, thin-walled with small trigones, leaf base without vitta-like area; cuticle smooth; oil bodies not observed. Underleaves present, very small, deeply bifid with ciliate lobes. Androecia not seen. Perianth without stalk, perianth mouth densely laciniate. Vegetative reproduction not seen.

#### NOTES

*Plagiochila strictifolia* (sect. *Vagae*) is recognized by the flaccid, dichotomously branched plants with mostly terminal branches, horizontally spreading, oblong-rectangular, non-ampliate, outwards-arching leaves with rounded to subtruncate, subentire apex, ± entire margins, small thin-walled cells, very shortly decurrent leaf bases and small underleaves. In its subentire leaves, *P. strictifolia* resembles *P. repanda* but the leaves in the latter species are ampliate, branches are very scarce and mostly intercalary, and the leaf cells have large, swollen trigones.

#### *Plagiochila terebrans* Nees & Mont. (Fig. 22)

*Plagiochila terebrans* Nees & Mont., *Species Hepaticarum* (fasc. 2-4): 98 (1840). — Type: **France**. La Réunion, *C. Richard s.n.* (lecto-, designated here, PC0699835 [=MB3436]!; isolecto-, PC0699833! [=MB3435]). In the protologue no collector is cited, but in Synopsis Hepaticarum (Gottsche *et al.* 1844: 36) Richard is cited as the collector of the type.

*Plagiochila angustissima* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 2 (12): 975 (1902). — Type: **Madagascar** (Jones 1962).

*Plagiochila berthieui* Steph., *Bulletin du Jardin botanique national de Belgique* 32: 36 (1893). — Type: **Madagascar** (Vanden Berghen 1981).

*Plagiochila borgenii* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 341 (1882), *nom. inval.* — Type: **Madagascar** (Grolle 1995).

*Plagiochila fissicalyx* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 2 (12): 970 (1902). — Type: **Madagascar** (Vanden Berghen 1981).

*Plagiochila hildebrandtii* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 2 (12): 982 (1902). — Type: **Madagascar** (Vanden Berghen 1981).

*Plagiochila laxifolia* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 339 (1882). — Type: **Madagascar** (Jones 1962; Grolle 1995).

*Plagiochila replicatula* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 2 (12): 982 (1902). — Type: **Madagascar** (Vanden Berghen 1981).

*Plagiochila sublinearis* Gottsche, *Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 7: 341 (1882). — Type: **Madagascar** (Grolle 1995).

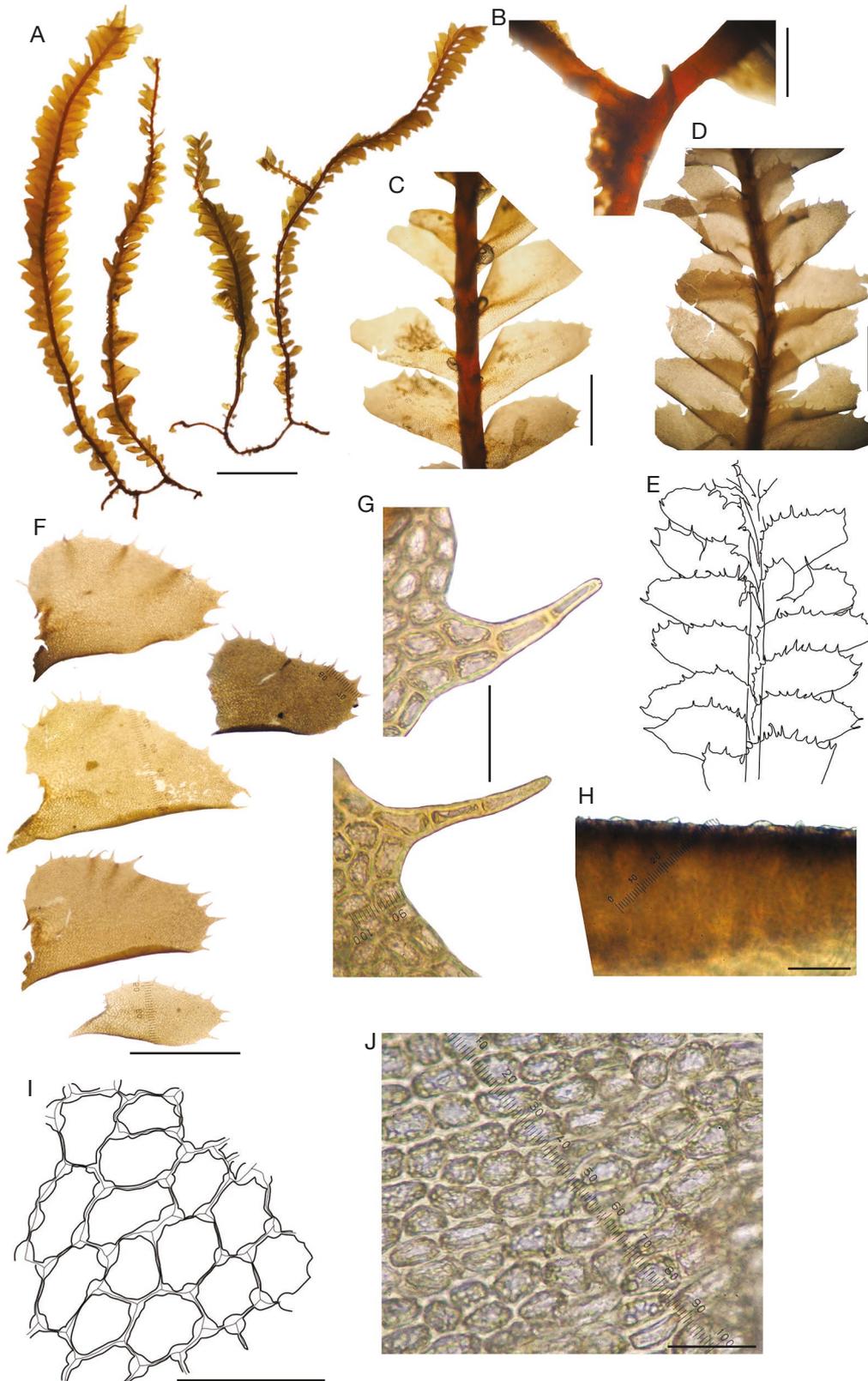


FIG. 20. — *Plagiobila stricta* Lindenb. (robust phenotype): **A**, habit; **B**, intercalary branching (leaves removed); **B, C**, shoot in dorsal view; **D, E**, shoot in ventral view; **F**, leaves; **G**, teeth of leaf margin; **H**, papillose cuticle; **I, J**, midleaf cells. From Bolivia, Lewis 83-3709 (GOET). Scale bars: **A**, 5 mm; **B, F**, 1 mm; **C-E**, 0.5 mm; **G-J**, 0.05 mm.

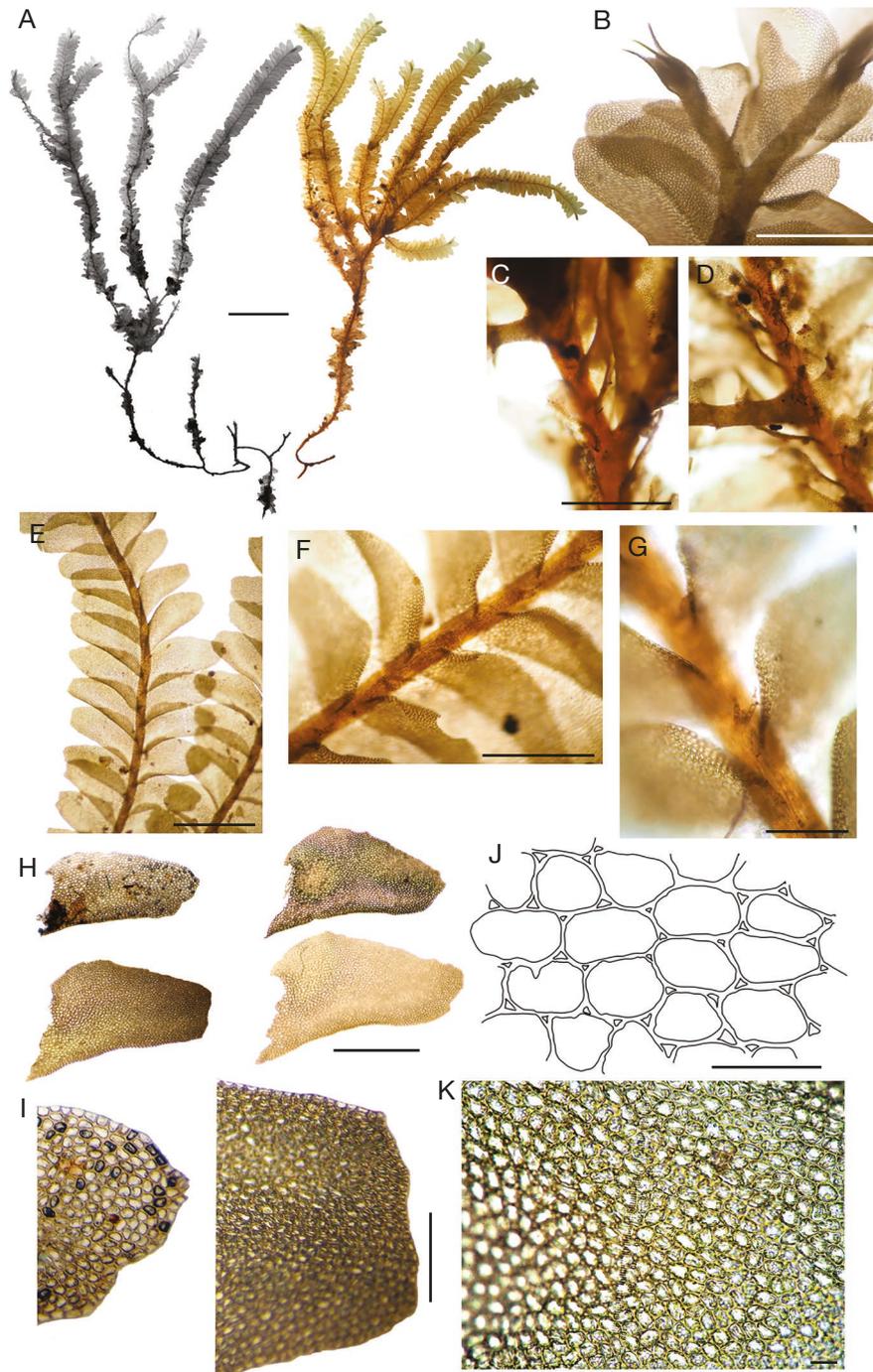


FIG. 21. — *Plagiochila strictifolia* Steph.: **A**, habit; **B**, terminal branching; **C**, shoot with terminal branch (lower) and intercalary branch (upper); **D**, shoot with intercalary branch; **E**, shoot in dorsal view; **F**, **G**, shoot in ventral view, showing underleaves; **H**, leaves; **I**, leaf apex; **J**, **K**, midleaf cells. From Pócs 9446/P (EGR). Scale bars: A, 5 mm; B-D, F, H, 0.5 mm; E, 1 mm; G, I, 0.25 mm; J, 0.025 mm; K, 0.05 mm.

ADDITIONAL SPECIMENS EXAMINED. — **Madagascar**. Forêt d'Amperifery, *Camponon 246* as "*P. rutenbergii* Gottsche" (PC). — **Prov. Antananarivo** • Angavokely, I.1978, *Tixier 11111, 11848* (BR); Analamanga, Angavokely Forest, I.2011, *Reeb 11M140, 11M152* (PC); Ankaratra, Manjakatempo Reserve, 1971, *Cremers 1683, 1694, 1711, 1742, 1744* (BR), *Pócs 9481/AH, Pócs 9481/D, 9481/R* (EGR); Mandraka, II.1974, *Onraedt 70M2174, 70M2183* (BR); Mandraka, Mt. Hantsambatonangavo, IX.1994, S. *Orbán 9452/CY* (EGR). — **Prov. Antsiranana** • Marojejy Nat. Park, Andampibe valley, III.1990, *Pócs et al. 90111/A* (EGR). — **Prov. Fianarantsoa** •

Nosiarivo, XI.1976, *Tixier 9546* (BR); Ambatofitorahana Forest S of Ambositra, *Onraedt 70M402, 70M.443, 70M5321, 70M5325, 70M5321, 70M5379* (BR); 33 km SSW of Ambositra, IX.1994, *Pócs 9479/C, 9479/G* (EGR, GOET); Andringitra Nat. Park, trail to Pic Boby, IX.1994, *Orbán 9458/AD* (EGR); W tributary of Korokoro river, IX.1994, *Pócs 9472/A, 9472/B, 9472/C, 9472/E, 9473/BB, 9473/BC, 9473/BE* (EGR); Ranomafana Nat. Park, Sahamalaotra Forest near Vohipara village, VII.2004, *Pócs et al. 04120/BW* (EGR, GOET); near Ambatolahy, XI.1994, *Pócs 9466/S* (EGR); beyond W park boundary, Mt. Namatoana, *Pócs & Tuba*

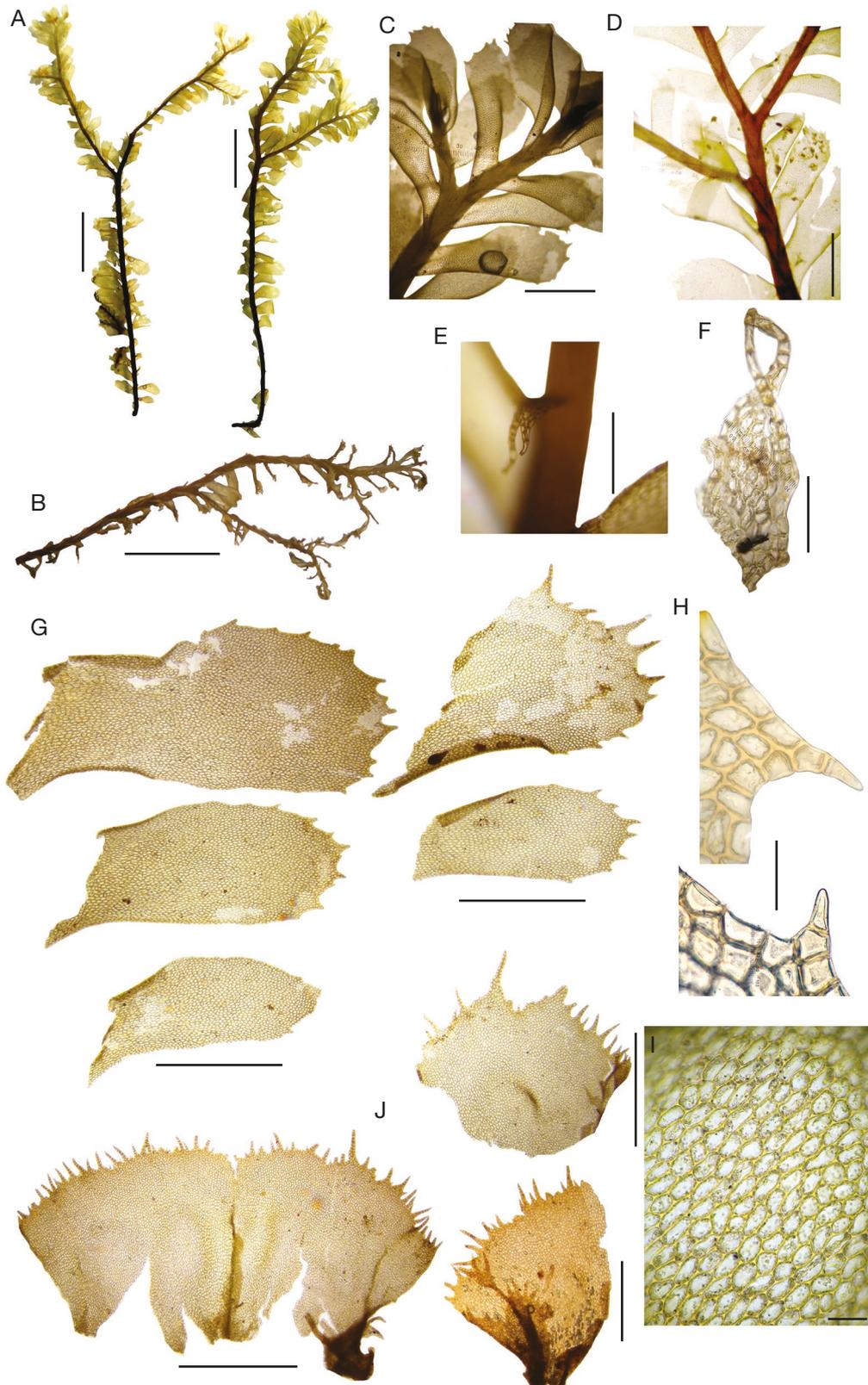


FIG. 22. — *Plagiochila terebrans* Nees & Mont.: **A**, habit; **B**, dried shoot showing leaves ventrad habit of leaves; **C**, **D**, shoots in dorsal view with terminal branches; **E**, shoot in ventral view, showing underleaf; **F**, underleaf; **G**, leaves; **H**, leaf apex; **I**, midleaf cells; **J**, female bracts and perianth. From Reeb CR11152 (PC). Scale bars: A, B, 5 mm; C, D, G, J, 1 mm; E, 0.5 mm; F, 0.1 mm; H, I, 0.05 mm.

04130/K (EGR). — **Prov. Toamasina** • East of Beforono, 600 m, III.1970, *Cremers 70M8061* (BR); W coast of Masoala Peninsula, S of Ambanizana village, IX.1994, *Pócs 9446/AD, 9446/GQ, 9449/H* (EGR); Andasibe-Mantadia Nat. Park, III.1990, *Pócs et al. 90103/AL, 90104/AB, 90105/D* (EGR), *9016/AG* (EGR, GOET); X.1994, *Pócs 9485/B* (EGR).

**DISTRIBUTION AND HABITAT.** — Widespread in tropical and southern Africa. In Madagascar on bark, rock, soil and rotten wood in humid to subhumid evergreen forests from sea level to 2150 m.

**DESCRIPTION** (see also Jones 1962; Vanden Berghen 1981; Wigginton 2004)

Plants *c.* 2–5 mm wide, to 5 cm long, very flaccid, dichotomous to irregularly pinnately branched, branches mostly terminal, basal branches sometimes intercalary, rhizome-like creeping shoot present. Mature stem leaves distant to contiguous to subimbricate, ventrad, obliquely to widely spreading, sometimes deflexed, asymmetrically ovate-oblong to ligulate or ovate-triangular, 1.5–3× longer than wide, widest in the lower third or middle, branch leaves not ampliate and not shouldered, ventral margin usually recurved in the lower half, older stem leaves ampliate or not ampliate; leaf margins unbordered, dorsal leaf margin entire, apex and ventral margin with 3–20 small to large triangular teeth, the tip cell of the teeth elongate, 2–4× longer than wide, often broken; leaf bases narrowly decurrent, dorsal base shortly to moderately decurrent, ventral base very shortly decurrent. Cells of branch leaves small, subrectangular and in rows, *c.* 14–20 µm wide in midleaf, *c.* 1.5× longer than wide, with small triangular or cordate trigones, on longer walls radiate and sometimes confluent; cells of older stem leaves larger and subsodiametrical, not in rows, 18–25 µm wide in midleaf, trigones larger and swollen, cells not forming a border; cells in the dorsal leaf base not conspicuously elongate, vitta-like area absent; cuticle smooth; oil bodies not observed. Underleaves lacking or very small. Androecia terminal or intercalary, with 4–12 pairs of bracts. Perianths campanulate, mouth with narrow laciniae, base not stalked. Vegetative reproduction by caducous leaves.

#### NOTES

*Plagiochila terebrans* (sect. *Vagae*) is a very common and variable species that is distinguished by the flaccid, dichotomous to irregularly pinnate plants with mostly terminal branches and with distant to subimbricate, ovate-oblong to ligulate leaves that are not ampliate to somewhat ampliate in basal stem leaves. The leaf margins have 3–20 triangular teeth with an elongate tip cell (2–4× longer than wide) and rather shortly decurrent bases, and the leaf cells are relatively small (15–25 µm wide in midleaf). Branch leaf cells are smaller than stem leaf cells and more elongate, subrectangular, ± arranged in rows.

*Plagiochila terebrans* may be confused with *P. pectinata*, but latter species lacks terminal branches and has leaves usually more strongly ventrad. *Plagiochila terebrans* approaches the neotropical *P. deflexinama* Taylor and *P. tamariscina* Steph. (Pócs 2006; Gradstein 2021), but branching in the latter two species is purely pinnate, not dichotomous, and caducous leaves are not produced.

### *Plagiochila vandenberghenii* Gradst., sp. nov. (Fig. 23)

*Plagiochila vandenberghenii* Gradst., sp. nov. (sect. *Vagae*) stands out by irregularly pinnate to dichotomous branching by terminal and intercalary branches, and somewhat distant, horizontally spreading, narrowly oblong-rectangular, non-ampliate leaves (*c.* 2.5–3× longer than wide) with the apex bifid by two large, lobe-like teeth, and a slightly bordered leaf margin with more elongate cells in 1–2 rows; 2–5 additional, smaller teeth are produced at the leaf apex and on the distal half of the ventral and dorsal margin. Underleaves are absent.

**HOLOTYPE.** — **Madagascar. Prov. Fianarantsoa** • Ranomafana Nat. Park, opposite park gate, near Ambodiamontana settlement, Namorona river valley, on bark in partially degraded lower montane rainforest, 865–1015 m, VII.2004, *Pócs et al. 04118/AY* (holo-, EGR!; iso-, GOET!).

**ADDITIONAL SPECIMEN EXAMINED.** — **Madagascar. Prov. Fianarantsoa** • Ranomafana Nat. Park, near park gate, 1067 m, on twigs, *Reeb CR17M610* (PC).

**ETYMOLOGY.** — Named after the late Professor Constant Vanden Berghen, renowned Belgian botanist and bryologist who has laid the basis for our knowledge of *Plagiochila* in Madagascar.

**DISTRIBUTION AND HABITAT.** — Only known from Ranomafana National Park (two collections) on Madagascar, growing on bark.

#### DESCRIPTION

Plants 3–4 mm wide, to 4 cm long, irregularly branched below and on broken shoots by intercalary branches, dichotomous above by terminal branches, rhizome-like creeping shoot present. Mature stem leaves distant to contiguous, widely and horizontally spreading (not ventrad), narrowly and subsymmetrically oblong-rectangular, 2.5–3× longer than wide, on branches up to 4× longer than wide, not caducous, not ampliate and not shouldered, margins almost parallel, unbordered or weakly bordered, with 5–8 teeth in the upper half made up of rectangular cells; leaf apex bifid by two long, lobe-like teeth, to 10–15 cells long, the two teeth separated by a wide rounded sinus, sometimes one of the two teeth is broken, a smaller tooth may be present in the sinus between the two large lobe-like teeth and occasionally the apex is trifid, tip cell of the teeth not much longer than the rest of the cells, distal portion of ventral and dorsal leaf margin with 1–3 smaller teeth, lower half of the margins and bases entire; leaf bases shortly and narrowly decurrent, the decurrent ventral part maximally 0.15 mm long. Leaf cells subsodiametrical to slightly elongate, 1–1.5× longer than wide, 18–30 µm wide in midleaf, trigones small but not swollen, triangular with concave walls and frequently radiate along the longer walls, cells along the margin sometimes more elongate and with a thicker inner tangential wall, forming a weak border, leaf base without vitta-like area, cuticle smooth; oil bodies not observed. Underleaves absent. Androecia not seen. Perianth campanulate, slightly elevated above the bracts on a short, thickened stalk. Vegetative reproduction not seen.

#### NOTES

*Plagiochila vandenberghenii* Gradst., sp. nov. (sect. *Vagae*) is readily distinguished from all other African members of the

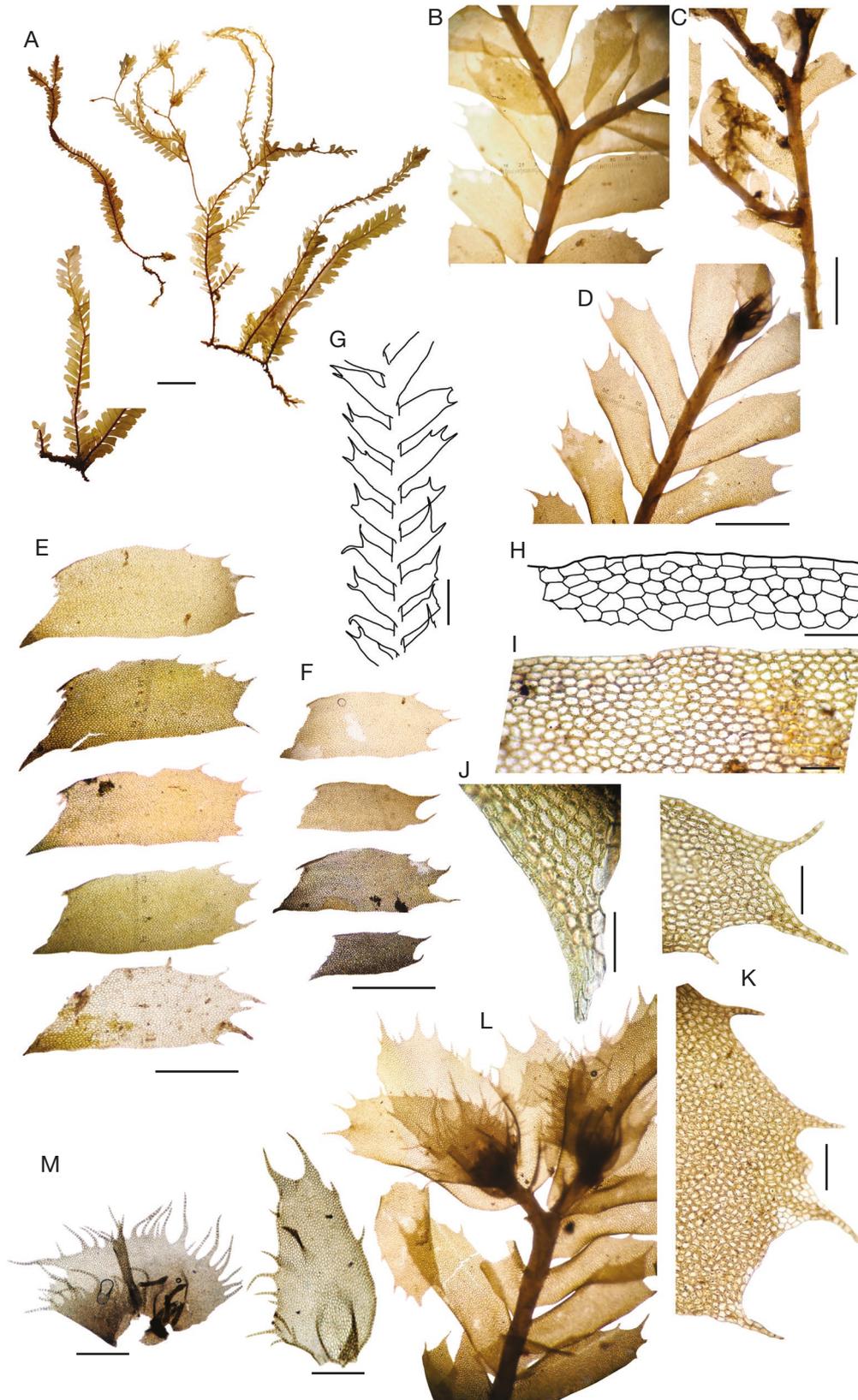


FIG. 23. — *Plagiochila vandenberghenii* Gradst., sp. nov.: **A**, shoots; **B**, shoot in dorsal view with terminal branching; **C**, intercalary branching; **D**, shoot in ventral view; **E**, stem leaves; **F**, branch leaves; **G**, branch in dorsal view; **H**, **I**, leaf margin cells; **J**, leaf base; **K**, leaf apex; **L**, shoot with perianth, two leaves at perianth base removed to show the perianth stalk; **M**, female bracts. From Reeb CR17M610 (PC). Scale bars: A, 5 mm; B-G, J, K, 1 mm; H, I, L, 0.1 mm; M, 0.025 mm.

genus *Plagiochila* by the horizontally spreading, narrowly oblong-rectangular, non-ampliate leaves (*c.* 2.5–3× longer than wide) with a strongly bifid apex, with two long teeth. In its horizontally spreading, bifid leaves, the new species cannot be confused with any other African species of *Plagiochila* and only resembles the Asian *P. bicornuta* Steph. (synonym: *P. laxissima* Schiffn.; *fide* So 2001), but the apical teeth in latter species are smaller and terminal branching is lacking.

The perianths in the new species are campanulate. According to Heinrichs (2002), campanulate perianths are characteristic of unfertilized gynoecea, but the perianths in *P. vandenberghenii* Gradst., sp. nov. had mature sporophytes.

#### FURTHER RECORD

##### *Plagiochila heterostipa* Steph.

*Plagiochila heterostipa* Steph., *Hedwigia* 31: 129 (1892). — Type: South Africa. Towriver, *Rehmann* 195 « original » (lecto-, designated as « type » by Jones [1962], G00045491!); Blanco, *Rehmann* 209 (paralecto-, G00113045).

#### NOTES

*Plagiochila heterostipa* (sect. *Vagae*), a species described from South Africa and widely reported from the African continent (Jones 1962; Fischer 2013), was reported from Madagascar by Jones (1962) based on a specimen in New York (leg. Parker, as *P. javanica*). Surprisingly, this record was not cited in Vanden Berghen (1981) and Grolle (1995). *Plagiochila heterostipa* is morphologically very similar to *P. terebrans* and only seems to differ in having less elongate leaves. In his annotation of the lectotype of *P. heterostipa*, E. W. Jones wrote (d.d. January 1958) “I suspect a depauperate form of *P. terebrans* to which it is certainly very close”. The taxonomic status of *P. heterostipa* and the record from Madagascar need further study.

#### EXCLUDED RECORDS

##### *Plagiochila boivinii* Steph.

*Plagiochila boivinii* Steph., *Bulletin de l'Herbier Boissier* (sér. 2) 2: 987 (1902). — Type: France. La Réunion, *Boivin s.n.*, ex hb. Bescherelle (lecto-, designated by Grolle [1995], G00045446!; isolecto-, G00065447 p.p.!).

DISTRIBUTION AND HABITAT. — Only known from La Réunion. Recorded from Madagascar by Vanden Berghen (1981), but these records belong to *P. incerta*.

#### NOTES

*Plagiochila boivinii* (sect. *Vagae*) is a species endemic to La Réunion that was recorded from Madagascar by Vanden Berghen (1981); the Madagassan records, however, belong to *P. incerta*. *Plagiochila incerta* clearly differs from *P. boivinii* in having ampliate leaves, leaf cells with large trigones and lack of underleaves. *Plagiochila boivinii*, on the other hand, has non-ampliate leaves, small trigones and distinct underleaves. The description and illustration of *P. boivinii* in Vanden Berghen (1981) is a mixture of *P. boivinii* and *P. incerta*.

##### *Plagiochila javanica* (Sw.) Nees & Mont.

*Jungermannia javanica* Sw., *Methodus Muscorum Illustrata*: 35 (1781). — *Plagiochila javanica* (Sw.) Nees & Mont., *Annales des Sciences naturelles, Botanique* (sér. 2) 5: 52 (1836). — Type: Java (Inoue 1984).

*Plagiochila calva* (Nees) Lindenb., *Species Hepaticarum* 1: 27 (1839). — *Jungermannia calva* Nees, *Enumeratio Plantarum Cryptogamicarum Javæ et Insularum Adjacentium* I: 70 (1830). — Type: Java (Inoue 1984).

#### NOTES

According to Jones (1962) and Grolle (1995), all African records of the common Asiatic *Plagiochila javanica* (sect. *Vagae*) should be erroneous. The species has been reported from Madagascar by Stephani (1894) and Dugas (1928), but the record of Dugas (as *P. calva*: leg. Camboué, PC) is *P. angusta* (Grolle [1995], however, identified it as *P. rodriguezii*); that of Stephani has not been revised. Jones (1962) identified a further *P. javanica* specimen from Madagascar (leg. Parker, New York) as *P. heterostipa* Steph., but the material probably belongs to *P. terebrans* (see above, under “Further record”).

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